Differentiation of morphology and reproductive traits in the House Finch (*Carpodacus mexicanus*): a comparison between native and introduced populations

by

Daniel R. Kozlovic, B. Sc., Toronto

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ABSTRACT

House Finches (Carpodacus mexicanus) were introduced to Long Island, New York from southern California in 1940. Apparently, an initial sample of less than 100 birds has given rise to a population that now occupies much of the eastern United States. This study was to determine if morphological and reproductive changes have taken place in introduced eastern birds, which have colonized a novel environment. A study area in Goleta, California (CAL) represented the parental population whereas for comparison, House Finches in St. Catharines, Ontario (ONT) represented the introduced population.

Interlocality variation in 25 morphometric characters of 100 adult House Finches was examined statistically. Single-classification analysis of variance revealed significant interlocality differentiation in seven characters of males and nine of females. Females showed differentiation in more limb elements than males. Analysis of character variation using discriminant and principal component analysis distinguished samples on the basis of variation in shape. Compared to CAL, ONT birds (especially females) had smaller extremities relative to certain core parts and weight. Females showed similar patterns of character covariation in each locality on the second principal component, which suggests that differentiation of the ONT population may not be solely environmentally induced. Sexual dimorphism was evident in four characters in ONT and five in CAL. Discriminant analysis distinguished sex on the basis of variation in shape. Males possessed a relatively larger flying apparatus

and smaller hind limbs than females. The degree of sexual dimorphism did not vary significantly between localities.

Data on reproductive parameters were collected in 1983 and 1984 in ONT, and 1984 in CAL. In 1984, House Finches began breeding approximately three months earlier in CAL than in ONT. In ONT, there was no significant difference in mean clutch initiation date between 1983 and 1984. In both localities most nests contained either four or five eggs, and clutch size differences between localites were not significant. Seasonal declines in clutch size were evident in ONT but not in CAL. Intralocality variation in egg weight and size was not related to clutch size. Egg weight showed no seasonal trend in ONT, but increased significantly with breeding season in CAL. In both localities egg weight increased significantly with order of laying in clutches of four but not in clutches of five. Eggs in ONT in 1983 and 1984 were significantly larger than in CAL in 1984. The modal incubation period was 13 days and did not vary significantly between localites. In both localities nestling weight on the day of hatching was correlated to fresh egg weight. For much of the period between hatching and 14 days post-hatch, ONT nestlings were significantly larger than CAL nestlings in terms of weight, bill length, bill depth, and manus length.

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INTRODUCTION

Although many species of birds have been introduced to regions outside their native range, there are only a few cases in which inoculum samples have given rise to major range expansions (Long 1981). Notable examples include the colonization of North America by House Sparrows (Passer domesticus, Barrows 1889; Wing 1943; Robbins 1973) and by European Starlings (Sturnus vulgaris, Wing 1943), both of which were introduced from Europe about 100 years ago. Lewontin and Birch (1966) regarded such range expansions as geographical (as distinct from ecological; see below) because the habitats being colonized were similar, in terms of climate and resource availability, to those from which the colonists originated. Geographical range expansion results from the removal of barriers to dispersal, or alteration of the habitat, usually by human presence.

Alternatively, an introduced species may subsequently colonize a distinct ecological regime (Mayr 1965). Indeed, ecological range expansions (Lewontin and Birch 1966) are probably facilitated by a variety of ecological, morphological, behavioural and genetic factors (Baker and Stebbins 1965) that may characterize certain individuals before or during the course of the range expansion. Such characteristics may be regarded as adaptations that enhance the ability of individuals to survive and reproduce under environmental conditions that were previously not encountered. Thus, major adaptive differentiation

may occur in response to novel selective pressures (Mayr 1965). Further, geographical differences in phenotypic traits may provide insight to the selective pressures that operate on populations.

Geographical variation in morphology

Studies concerning the evolutionary basis for morphometric variation among species are based on the notion that an organism's morphology reflects its ecology (Hespenheide 1973; James 1982; Lederer 1984; Leisler and Winkler 1985). Support for such an hypothesis is provided by plausible functional explanations for observed differences among species. For example, food-handling skills, and the range and size of food items available to different species of Darwin's finches, vary as a function of bill size (Abbott *et al*. 1977; Grant 1981). Species with large bills were able to eat larger and harder seeds than species with small bills. Thus, morphology is believed to be important in determining how an organism interacts with its environment. Similarly, environmental factors may account for morphological differences within a species. For example, population differences in bill length and body size of the Sharp-billed Ground Finch (*Geospiza difficilis*) appear to be related to particular dietary niches on different islands of the Galapagos (Schluter and Grant 1984).

Many species of birds show similar patterns of geographical size variation (Rensch 1960; James 1970). Of these, larger individuals tend to occur at higher latitudes where environmental

conditions are cooler, drier and evaporation is greatest (Johnston and Selander 1971; Power 1969, 1970; James 1970). Further, geographical size differences may be accompanied by corresponding changes in the proportioning of body parts; relative to body core parts, appendages tend to be smaller in individuals inhabiting cooler climates (Mayr 1956; Johnston and Selander 1971; Johnston 1973; Niles 1973). Such patterns of morphological variation suggest adaptation to the physical environment and have provided support for certain morphological generalizations. Bergmann's Rule (summarized by James 1970) for example, proposes that homeotherms are larger in cooler regions because the lower surface-to-volume ratio of a large individual reduces heat loss. Allen's Rule (summarized by Mayr 1970), a corollary of Bergmann's Rule, stresses the thermoregulatory dicates of size in body core parts relative to appendages. Thus, smaller appendages relative to body core parts may further reduce the surface-to-volume ratio, and thus loss of heat.

If patterns of geographical variation in the morphology of individuals represent adaptation to climatic conditions, then changes in average weather conditions (e.g. temperature) may be expected to alter morphology, and thus provide insight into the selective forces mediating morphology. Bumpus (1899) assessed the effects of a severe winter storm on a population of House Sparrows and found that males were subject to directional selection for increased size, while females were subject to stabilizing selection. Subsequent studies (Johnston and

Fleischer 1981; Fleischer and Johnston 1984) have noted similar differential selection on body size of House Sparrows, which is most intense in winter. Boag and Grant (1981) examined the effects of a drought on a population of Darwin's Finches (Geospiza fortis) in the Galapagos. They found that larger individuals survived best and attributed the directional selection on body size to food availability during the drought. Large and hard seeds predominated during the drought, and thus were available only to large individuals that could crack them. Collectively, these studies provide some of the best evidence for morphological adaptation in response to prevailing environmental conditions.

Since their introduction to North America in 1852, House Sparrows have differentiated significantly in weight and overall body size, which correlates strongly with geographical and climatic variables (Johnston and Selander 1964, 1971, 1973). Such differentiation became obvious 50 years following introduction, which indicates a rapid morphological adjustment to local environments. Further, patterns of character covariation in North American House Sparrows have been found to be similar in ancestral European (Johnston 1973) and introduced New Zealand (Baker 1980) populations; adaptive differentiation has been proposed for these observed geographical differences.

Geographical variation in breeding biology

Geographical comparisons of the breeding biology of birds have largely centred on describing differences in clutch size among geographically distinct populations. In many cases, clutch

size has been found to be positively correlated with latitude (Klomp 1970), and Lack (1954) suggested that such geographical differences could result from environmental limitations on the efficiency of parental foraging. Since day-length increases with latitude, birds breeding in northern environments have correspondingly more time to feed nestlings, and as a result may be able to raise larger broods. Ashmole (1963) related clutch size to the availability of food resources relative to the breeding density of the population. Since population numbers are more likely to fluctuate in more seasonal, northern environments due to winter mortality, ample food resources may be available the following spring allowing survivors to rear larger broods. Empirical data on clutch size and primary productivity (Ricklefs 1980; Koenig 1984) support Ashmole's (loc. cit.) results.

However, few studies have assessed geographical differences in reproductive traits of birds other than clutch size. Murphy (1978) compared the breeding phenologies and reproductive output of House Sparrows breeding in Calgary, Alberta and Lawrence, Kansas. Differentiation in breeding ecology between the two localities was limited mainly to differences in the timing of breeding and the probability that a clutch would be successfully incubated. Breeding began sooner in Lawrence than in Calgary, however, intralocality variance was high and interlocality variance low for most aspects of reproductive output. Murphy concluded that proximate factors of food availability and prevailing weather conditions adequately explained locality differences in reproductive traits in contrast to an adaptive

explanation based on geographic differences in the two populations.

Murphy (1983) compared aspects of the reproductive biology of Eastern Kingbirds (Tyrannus tyrannus) breeding in New York and Kansas. He found that weather had an important effect on the breeding biology of Kingbirds, but noted little geographical variation in most reproductive traits. Eggs were significantly heavier in New York than in Kansas, but their weights were not related to adult body size. Kingbird reproduction did not appear to be adapted to differences in average weather condititons between the two localities, but instead was largely affected by the prevailing, local weather conditions.

King and Hubbard (1981) compared growth rates of White-crowned Sparrows (Zonotrichia leucophris) among six sample populations from subarctic, subalpine, and low altitude montain habitats. They found that growth rate was invariant among the populations, consistent with the idea of a physiological maximization of growth (Ricklefs 1973). Thus, growth rate did not appear to be adapted in relation to local environmental conditions. King and Hubbard claimed that locality differences in the body weight of nestlings were "undoubtedly related at least in part to differences of adult body size", implying that heavier young were the product of heavier or larger adults. However, the relationship was not verified statistically.

House Finches (Carpodacus mexicanus) are indigenous throughout much of western North American from southern British Columbia to southern Mexico (Woods 1968). They prefer

warm, dry climates, are most abundant along the coastal lowlands of central and southern California, and while "most numerous about towns and cultivated lands" (Woods 1968), also inhabit wastes and deserts. In southern California the House Finch is considered the most common native passerine (Garrett and Dunn 1981).

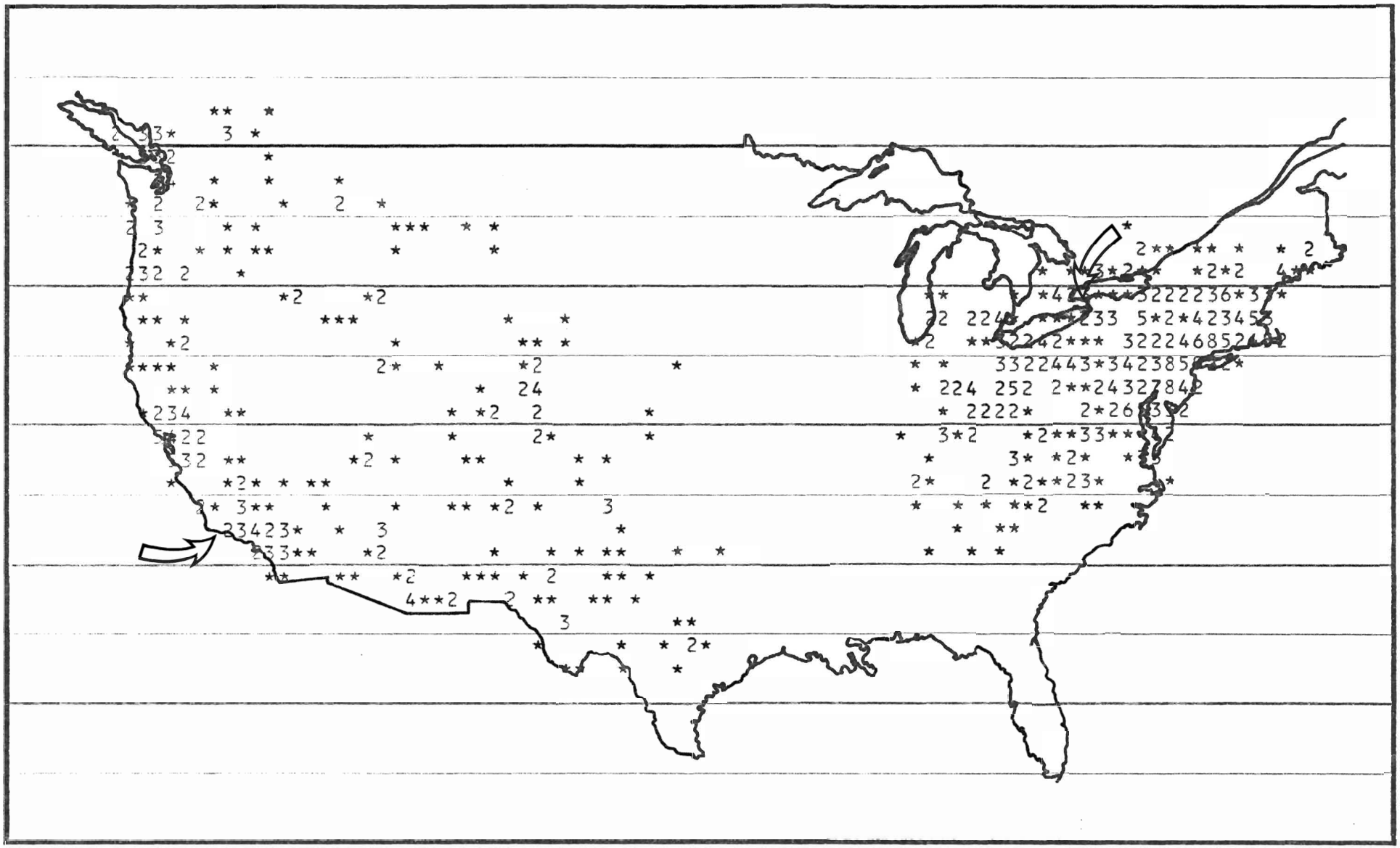
The subspecies C. m. frontalis has become established in both the Hawaiian Islands and eastern United States as a result of introductions. House Finches brought to Hawaii from California escaped from captivity before 1870 (Caum 1933) and by 1902 were common on the island of Maui (McGregor 1902). They are now abundant on all the major islands of the archipelago (Berger 1981). During the period 1930-1940 House Finches from the Los Angeles, California area were shipped by cage-bird dealers to many eastern states (Elliott and Arbib 1953). So intense was the traffiking that in 1940 the United States Fish and Game Department imposed a ban on further trade. Apparently, some of the remaining captive birds, which had no marketable value, were released (Elliott and Arbib 1953). Less than 100 birds in total were liberated in the towns of Massapequa, Hicksville, and Hewlett, Long Island in 1940, the Hewlett release site involving the least number of birds (R.S. Arbib, Jr., pers. comm.). By 1951 the population on Long Island had increased to an estimated 280 individuals (Elliott and Arbib 1953).

Subsequent range expansion throughout eastern North America from 1968-1980 was documented by Bystrak (1981), and by Mundinger and Hope (1982) for the period 1947-1979. House Finches were

reported in southern Connecticut and the New York City area east of the Hudson River between 1947-1954, and disjunct populations were established in northeastern Long Island, Pennsylvania and New Jersey by 1959. Continued range expansion, primarily in a southwesterly direction, was rapid along the Atlantic coastline and major New England rivers. By 1980 House Finches were reported breeding from southern Maine to the Carolinas and inland as far as Ohio (Bystrak 1981). The first nest in Ontario was discovered in Niagara-on-the-Lake in 1978 (James 1978). Brumal sightings in the United States and Canada in 1984 are shown in Fig. 1. Sightings in Michigan and south to northern Alabama and Georgia indicate continued range expansion primarily to the south and west.

I chose to assess the geographical variation in morphology and reproductive parameters of the House Finch at two extremes of the geographical range. My objective was to determine if morphological and reproductive differences could be identified between individuals in the parental California population, and those that have colonized a novel environment in southern Ontario. In so doing, I ask the following question, "do differences in the introduced population suggest adaptive differentiation in response to local environmental conditions?"

Figure 1. Brumal sightings of House Finches in the United States and Canada in 1984 and 1985 during the 85th Christmas Bird Count (CBC, American Birds 1985). Each asterisk denotes a CBC on which House Finches were sighted and numerals indicate the number of CBCs (asterisks) in a given area. Arrows indicate study areas (see materials and methods).



MATERIALS AND METHODS

The Study Areas

The two populations that were studied were located in St. Catharines, Regional Municipality of Niagara, Ontario (ONT; 43° 10' N, 79° 15' W) and Goleta, Santa Barbara County, California (CAL, 34° 25' N, 119° 41' W) (Fig. 1; see Appendix 1). The study sites were restricted to urban centres near open water. Habitat in both locations was similar, which consisted entirely of residential areas with manicured lawns and ornamental hedges, shrubs and trees.

In ONT favoured breeding areas included neighbourhoods with wide, open streets and numerous spruce (Picea pungeus), juniper (Juniperus chinensis, J. scopulorum, J. virginiana) and cedar (Thuja occidentalis) while in CAL similar neighbourhoods were decorated with yucca (Yucca aloifolia), twisted juniper (J. chinensis), Italian cypress (Cupressus sempervirens), and palm (Washingtonia filifera). Thus, it was possible to restrict surveys to several relatively small regions in each locality.

The study areas were surveyed daily between 07:00 and 15:00 from 17 May to 3 August in 1983 (ONT), 25 May to 7 August in 1984 (ONT) and 2 March to 20 May in 1984 (CAL). Since the breeding season of House Finches in southern California begins about three months earlier than in ONT, it was possible to survey both the ONT and CAL study areas in 1984.

Data Collection

Climates

Climatic data for ONT and CAL were obtained from the Ontario Climate Centre Microfiche Records for the period 1940-84 and Climatological Data, California (see Appendix 2 for listing of agencies) for the period 1950-83, respectively. Climatic data for CAL in 1984 were obtained from the Flight Service Station at the Santa Barbara Municipal Airport for the months January-April and days 1 May-17 May. Mean monthly temperature (^{o}C) and total monthly precipitation (mm) were used to assess interlocality variation in climate. These climatological data were obtained from weather stations at the Niagara District Airport, Ontario, at Jordan Station, Ontario and at Santa Barbara Municipal Airport, which were selected because of their completeness of records and proximity to the respective study sites.

Morphometrics

In 1984, 100 adult House Finches were collected between 22 January - 15 February (ONT) and 8 March - 9 March (CAL). Twenty-five individuals of each sex were either caught with mist nets or ground traps at each location. These specimens were prepared as skins and skeletons at the Royal Ontario Museum, Toronto, Ontario. Specimen preparators determined qualitatively the amount of cutaneous and visceral body fat of each specimen as one of four categories: nil, light, moderate, heavy (Appendix 3). Adults were distinguished from juveniles by their wider and less conspicuous ventral streaking, and white rather than buffy-tipped wing coverts (Woods 1968). Specimens were verified as being

adults by the presence of complete cranial ossification in all birds (Nero 1951).

Twenty-nine characters were measured on each specimen (19 skeletal, 9 external, and weight). The characters and their abbreviations are given in Table 1 and described in Appendix 4. Linear measurements were made to the nearest 0.05 mm, with dial calipers, except for WLP and WLS that were measured to the nearest 0.5 mm , with a rule. The fresh weight of each specimen was measured to the nearest 0.25 g using a 50-g Pesola spring scale and the cube root of weight determined.

Nesting biology

Nests were not difficult to find. Observations on singing males and individuals carrying nesting material were usually indicative of a nest nearby in the area. A search of suitable nest trees usually revealed the nest. A total of 218 nests was found, 106 in ONT (66 in 1983, 40 in 1984) and 112 in CAL. However, many nests in ONT were difficult to reach because of their placement in the tops of tall conifers. Thus, for practical purposes, only nests that were accessible with a six-foot (1.9 m) stepladder were studied, which included 48 nests in ONT (27 in 1983, 21 in 1984) and 81 in CAL. Nests were observed to determine dates of clutch initiation, order of eggs within a clutch, clutch and egg sizes, and to measure nestling growth.

The date of clutch initiation was determined explicitly by observation of the first egg laid and implicitly by backdating.

Table 1. Morphological characters and their abbreviations.

Character	Abbreviation
Skeletal	
Skull length	SKUL
Skull width	SKUW
Skull depth	SKUD
Premaxilla length	PREL
Premaxilla depth	PRED
Mandible length	MANL
Mandible symphysis length	MASL
Mandible depth	MAND
Coracoid length	CORL
Sternum length	STEL
Keel depth	KEED
Humerus length	HUML
Ulna length	ULNL
Pelvis length	PELL
Pelvis width	PELW
Femur length	FEML
Tibia length	TIBL
Tarsometatarsus length	TARL
External	
Tip of bill to nostril length	BNL
Exposed bill length	BIL
Bill depth	BID

Bill width, upper rhamphothecus	BWU
Bill width, lower rhamphothecus	BWL
Wing length to the longest primary	WLP
Wing length to the longest secondary	WLS
Tail length	TLL
Tarsometatarsus length	TSL
Weight	
Fresh weight	WEI
Cube root of weight	CWEI

Clutch completion required four to five days (one egg per day) as the usual clutch sizes were four and five. The modal incubation period from the laying of the last egg to its hatching was 13 days in ONT (23 nests) and CAL (20 nests) and ranged from 12 to 15 days. Therefore, a total of 17 or 18 days, depending on clutch size, was required from the laying of the first egg to the completion of incubation.

Eggs were numbered as they were laid and their maximum length, breadth and fresh weight (taken on day of laying) were determined. Linear measurements and weight were taken to the nearest 0.05 mm and 0.05 g with dial calipers and a 5-g Pesola spring scale, respectively. In 1983 (ONT) egg weights were not taken, however, fresh egg weight was calculated from egg volume (see below). In addition, egg length and breadth were taken from 284 eggs (64 clutches) from Los Angeles County, California and 85 eggs (17 clutches) from Oregon at the Western Foundation of Vertebrate Zoology, Los Angeles, California.

Egg volume was equated to fresh egg weight by the relation

$$C (L * B^2) = \text{fresh egg weight}$$

where L is egg length, B is egg breadth and C is a constant. The C values determined from 82 and 263 eggs were 0.531 (ONT, 1984) and 0.533 (CAL), respectively. Linear regressions of fresh egg weight on egg volume explained 98% (ONT) and 96% (CAL) of the variation in fresh egg weight (ONT: Pearson product-moment coefficient of correlation, $r = 0.99$, $Y = 0.495X + 0.148$, $P << 0.001$; CAL: $r = 0.98$, $Y = 0.548X - 0.055$, $P << 0.001$).

Therefore, egg length and breadth were used to determine the fresh egg weight of museum eggs from Los Angeles County and Oregon (C = 0.533) and ONT in 1983 (C = 0.531).

During the nestling period, nests were observed on a daily basis. At hatching, nestlings were marked by clipping a toenail allowing individual recognition within each nest. The following characters were measured at approximately the same time each day between 07:00 and 15:00: bill length (from the anterior margin of the nostril to the tip of the bill), bill depth (from the lower margin of the lower rhamphothecus to the upper margin of the upper rhamphothecus at the base of the bill), manus length (from the base of the alula to the fleshy distal margin of the manus), wing length (from the anterior margin of the closed wing to the longest developing primary), tarsometatarsus length (from the notch at the tibiotarsal-tarsometatarsal joint to the distal bend of the basal phylanges), and weight. Linear measurements were made to the nearest 0.05 mm, with dial calipers, except for wing length that was measured to the nearest 0.5 mm, with a rule. Weight was measured to the nearest 0.1 and 0.25 g using 10 and 50-g Pesola spring scales, respectively. Measurements were made from hatching (day = 0) until the nestlings were 14 days of age.

Cowbird parasitism

House Finch nests found in ONT commonly contained a Brown-headed Cowbird (Molothrus ater) egg, although such parasitism was not observed in CAL. In 1983 parasitised nests were observed to determine their outcome. Virtually all cowbird nestlings perished several days after hatching. Since cowbird

eggs ususally hatched one or two days before those of their host's, parasitism did not affect post hatching development of House Finch young, so subsequent cowbird eggs that were encountered were not removed from the nest. Parasitism did complicate clutch size determination since a cowbird may remove one or more host eggs (Bent 1958), and therefore nests that were found containing one or several cowbird eggs were not used in clutch size analyses.

Data presentation and statistical treatment

Parametric assumptions of normality (g_1 , skewness; g_2 , kurtosis) and homogeneity of variance (Bartlett-Box test and Levene test or F-max test) were generally met. When the variances were heterogeneous, separate variance estimate t-tests and the Brown-Forsythe (1974) adjusted F were used. Most computations were carried out using the SPSS (Nie et al. 1975; Hull and Nie 1981) and BMDP (Dixon 1985) series of statistical programs on the Burroughs B7900 computer at Brock University.

Climates

Climatic data are presented as mean monthly temperature and precipitation for ONT and CAL. Means did not include weather data from survey years.

Morphometrics

Missing values (characters broken) accounted for 1.9% of the total data matrix and were estimated by multiple regression (all possible subsets method). Estimates were used only from

regressions with adjusted, squared multiple correlation coefficients greater than 0.70. Otherwise missing values were replaced by the mean for that character. Only one character, SKUD, was missing more than four of the 25 values and was not included in the analyses. The repeatability of skeletal character measurements was determined by expressing the difference between each character score and a mean of scores (N = 3) as a percent of a mean of scores. Fifteen specimens were remeasured three times to generate a mean for each character from which mean percent repeatabilities for each character were calculated. All skeletal character measurements were highly repeatable (Appendix 5). However, characters that I considered to be unreliable, namely PRED, MANL, and MASL, were not included in the analyses. PRED proved to be a difficult character to measure, and thus its repeatability among specimens was questionable. Similarly, MANL and MASL were not included in the analyses because it was often difficult to determine if the mandible was entire given its brittle, anterior margin.

In all cases skeletal and external character suites were analysed separately using multivariate and univariate procedures. Unlike single-classification tests, multivariate techniques consider variation in all characters simultaneously and are extremely sensitive to outliers. Multivariate outliers are cases that have atypical combinations of scores. Such cases are difficult to detect because the characters may be normally distributed when considered singly. Multivariate outliers were tested among the characters by determining the Mahalanobis

(generalized) distance from each case to the centroid (the "mean" of the sample in an n-dimensional space for n characters) of all cases in each sample. The Mahalanobis distance, analagous to the univariate z-score, is a chi square variable. The critical value for identifying outliers is chi square divided by degrees of freedom (number of characters in suite) at the desired alpha level. There are several methods of dealing with outliers, the most expedient being the deletion of cases. A search for outliers revealed that all cases had distance values below the critical value (2.000, df=16 for skeletal characters and weight; 2.321, df=10 for external characters and weight) at the 0.01 alpha level. Thus, all specimens collected were used in subsequent analyses.

Sexual dimorphism in each locality was assessed multivariately using a one-way multivariate analysis of variance design (MANOVA, Wilk's determinant ratio method) between the sexes. MANOVA was also used to test for interlocality variation in skeletal and external suites of characters. MANOVA comparisons between sex and location were followed by single classification analysis of variance (ANOVA) for each character and discriminant functions analysis (DFA, Cooley and Lohnes 1971).

Discriminant functions analysis is a multivariate statistical procedure that establishes the linear combination(s), the discriminant function(s), that best separate among groups. The technique is analagous to a single classification ANOVA. Associated with the DFA is a MANOVA that calculates a statistic

(Wilk's lambda (λ)) that is the quotient of the matrix of deviations of cases from their group centroids, divided by the matrix of deviations of cases from the grand mean:

$$\lambda = \left| \frac{W}{T} \right|$$

(Cooley and Lohnes 1971). Therefore, the greater the difference among groups, the smaller the value of λ. The significance of the difference among groups was determined by Rao's F approximation of λ that was compared against an F distribution (Cooley and Lohnes 1971). Although MANOVA determines the significance of the difference among group centroids, DFA identifies the characters that contribute to this difference, and classifies the cases in the samples.

Interlocality variation in sexual dimorphism was examined using discriminant analysis on skeletal characters and weight. All samples (males and females from ONT and CAL) were entered into a single, direct DFA. The difference in individual DF scores between sex for each locality was then compared between localities using a t-test.

Covariation among skeletal and external characters was assessed using principal components analysis (PCA). PCA is an extremely useful technique for data reduction. Given a matrix of correlations for a set of characters, PCA enables underlying intercorrelations in the data to be expressed as a reduced set of independent dimensions (principal components) that explain most of the variance in the original data matrix (Cooley and Lohnes

1971). Thus, PCA summarizes the information about intercorrelations among characters.

In PCA, eigenvalues and their associated eigenvectors (characteristic roots and vectors) were extracted from the correlation matrices (Appendix 6). In an $n \times n$ matrix there are n eigenvalues, the sum of which is equal to the total variance in the n-dimensional space. The first eigenvalue (λ_1) explains most of the variation in the correlation matrix and is identified as the largest eigenvalue. The first eigenvalue and its corresponding eigenvector define the first principal component (PC I). The second eigenvalue (λ_2) and associated eigenvector (PC II) is orthogonal to λ_1 and explains the second largest amount of variation in the matrix, and so forth. Since the total amount of variation in the matrix is equal to n characters, eigenvalues that are less than one (1) explain less variation that any character alone. Therefore, PCs with corresponding eigenvalues greater than one were extracted from the correlation matrices (Kaiser 1960).

PCA was used to ordinate cases in a multivariate hyperspace. The position of each case in n-dimensions (characters) was projected onto the respective principal components as component scores. Between locality t-tests were then performed using individual component scores of the first three principal components.

Nesting biology

Sample sizes varied according to available data and analyses used. Comparisons of means of egg characters among samples were

made using ANOVA and then by arranging the means in decreasing order of their magnitude and determining non-significant sets of means using t-tests. This procedure decreases the number of comparisons to be made and is an alternative to simultaneous test procedures (STP) when variances are heterogeneous.

Variation in nestling size was assessed multivariately using MANOVA (Wilk's determinant ratio method) followed by ANOVA on single characters. Comparisons among populations were made using nestlings of age 0 (at hatching), three, six, nine and 13 days. Unplanned comparisons of means were made using the Scheffe's STP a posteriori option of ANOVA.

Of the 864 nestlings used in population comparisons, 16 (1.9%) had Mahalanobis distances that exceeded the critical chi square (3.017, df = 5) at the 0.01 level of significance and were removed from analyses (see morphometrics section in materials and methods). However, cases identified as outliers represent only a small fraction of each sample (ONT 1983: 3/252 (1.2%); ONT 1984: 3/133 (2.2%); CAL 1984: 10/466 (2.1%)), and thus inferences may be extended to the original samples.

Variation in nestling growth among brood sizes of nestlings at hatching, three, six, nine and 13 days was assessed using two-way factorial ANOVA on ONT data with year and brood size as main effects and single classification ANOVA on CAL data. Although broods ranged in size from one to six nestlings, only those nests containing three, four or five individuals were included in analyses because sample sizes for broods containing one, two or six nestlings were too small. Brood size was

determined as the number of young present in a nest at any given time. Therefore, broods that experienced a reduction in size due to mortality of individuals were reclassified, accordingly. Brood reductions in ONT occurred in 4/20 (1983) and 5/11 (1984) nests, and in CAL in 13/34 nests.

RESULTS

Climates

Interlocality variation in annual temperature (Fig. 2) and precipitation (Fig. 3) is marked. The climate of CAL is characterized by mild temperatures throughout the year, maximum rainfall in winter, and relatively dry summers. Bailey (1960, 1964 in Climates of North America 1974) regards the climate of coastal California as the most temperate of the conterminous United States.

The climate of ONT is typically continental. Mean January temperatures are as low as -4 °C, while mean July temperatures exceed +20 °C (Fig. 2). ONT lies in a region of seasonally well-distributed precipitation (Fig. 3). Winter precipitation occurs as rain, freezing rain or snow, with total annual snowfall averaging approximately 120 cm (Climates of North America 1974). The Great Lakes affect the climate of the immediate area (Changnon and Jones 1972); for example snowbelts occur to the east of the five lakes where seasonal snowfalls may reach 400 cm (Muller 1966).

Mean monthly temperature and precipitation during the study periods are compared with long-term averages of 33 years for CAL and 42 years for ONT in Fig. 4. During the winter and spring of 1984, CAL weather had relatively high temperatures during the period March-May and low precipitation for the months February-April. ONT experienced normal temperatures throughout the breeding months of 1983 and 1984 although it was warmer than usual in July of 1983. Mean monthly precipitation, unusually

Figure 2. Mean monthly air temperature calculated from data covering the period 1940-1982 in ONT (solid circles) and 1950-1983 in CAL (open circles). Vertical bars indicate ± 1 standard deviation.

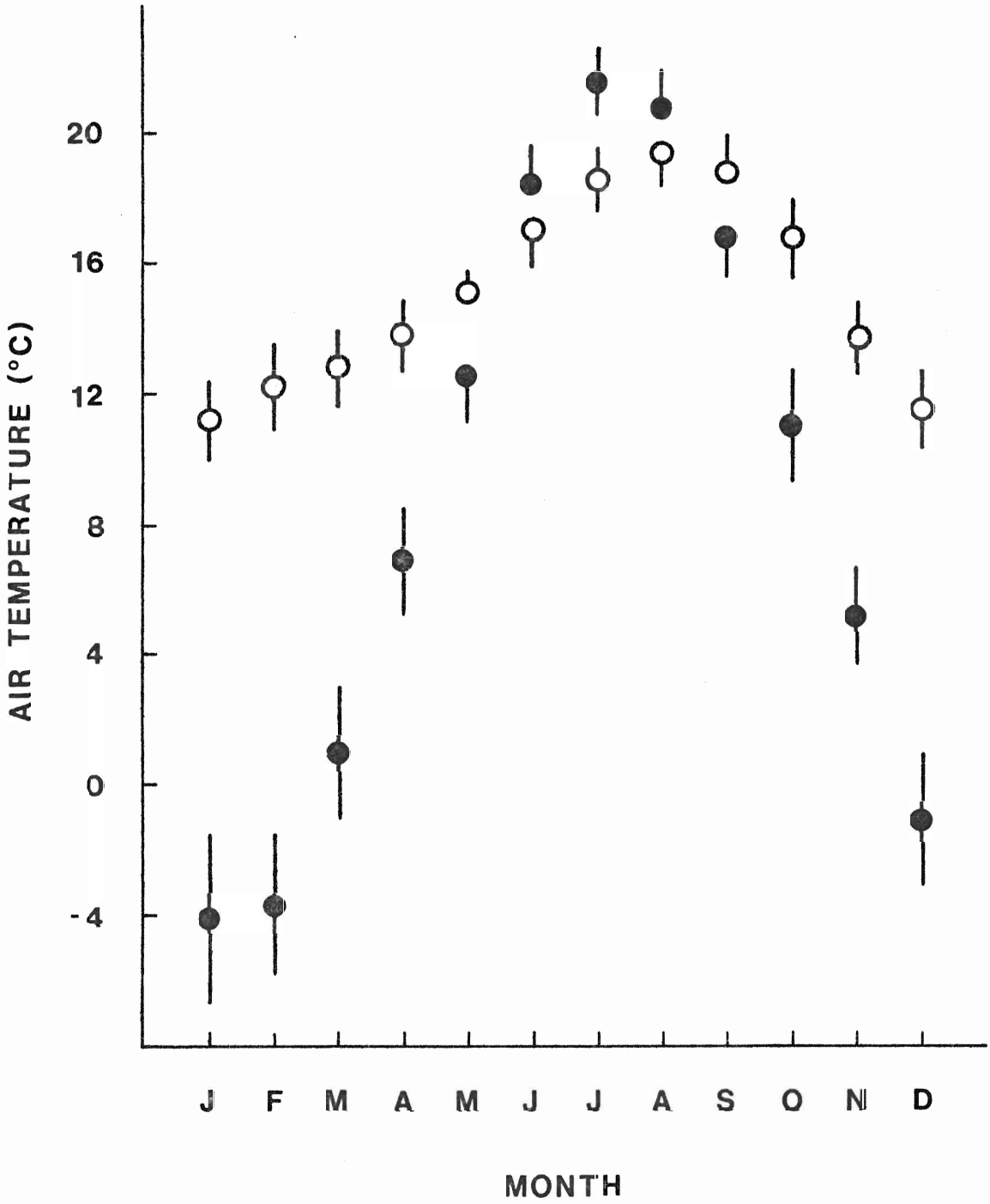

AIR TEMPERATURE (°C)
20
16
12
8
4
0
-4
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Figure 3. Mean monthly precipitation calculated from data covering the period 1940-1982 in ONT (shaded bars) and 1950-1983 in CAL (solid bars). Vertical lines over bars indicate ± 1 standard error.

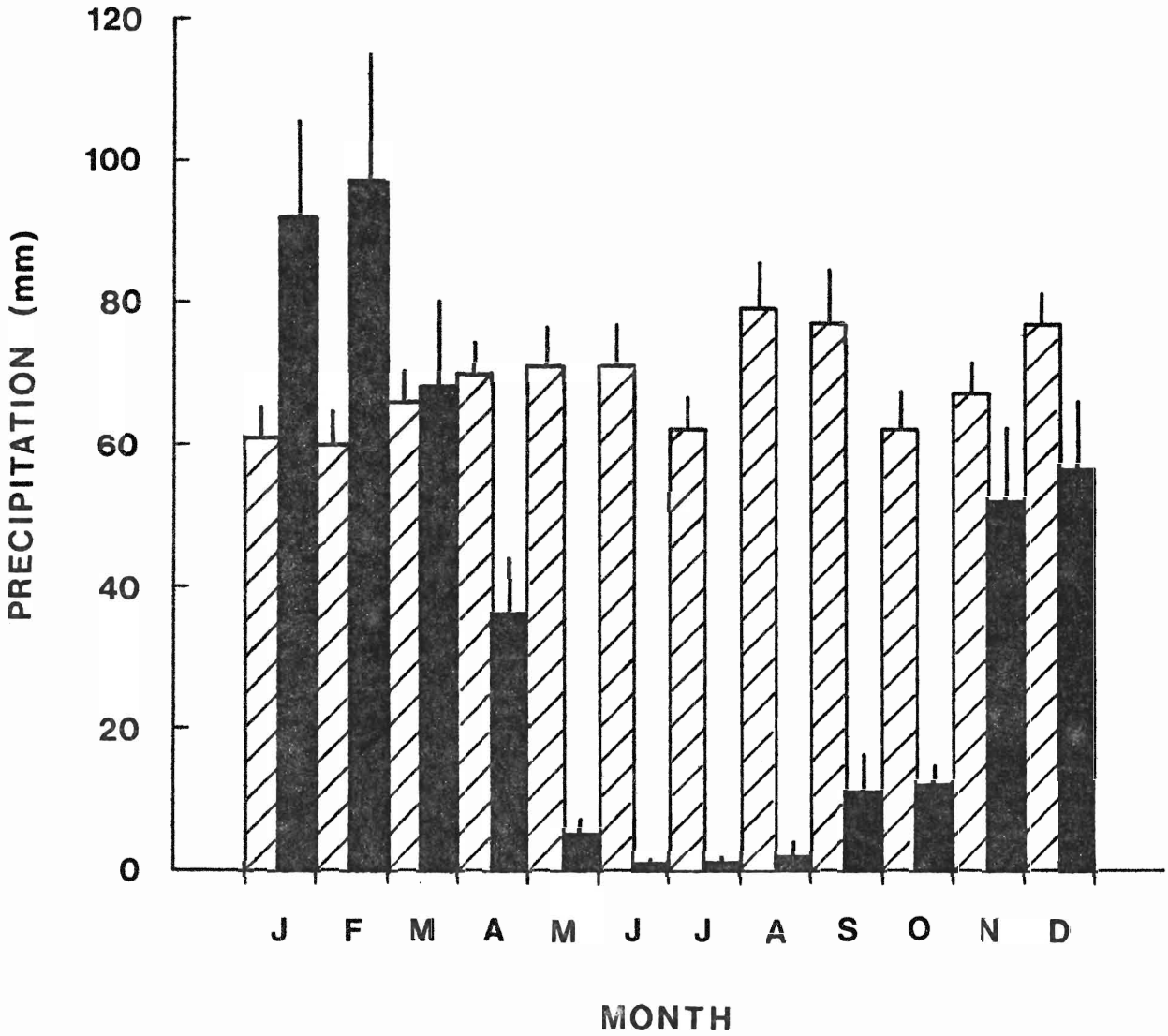
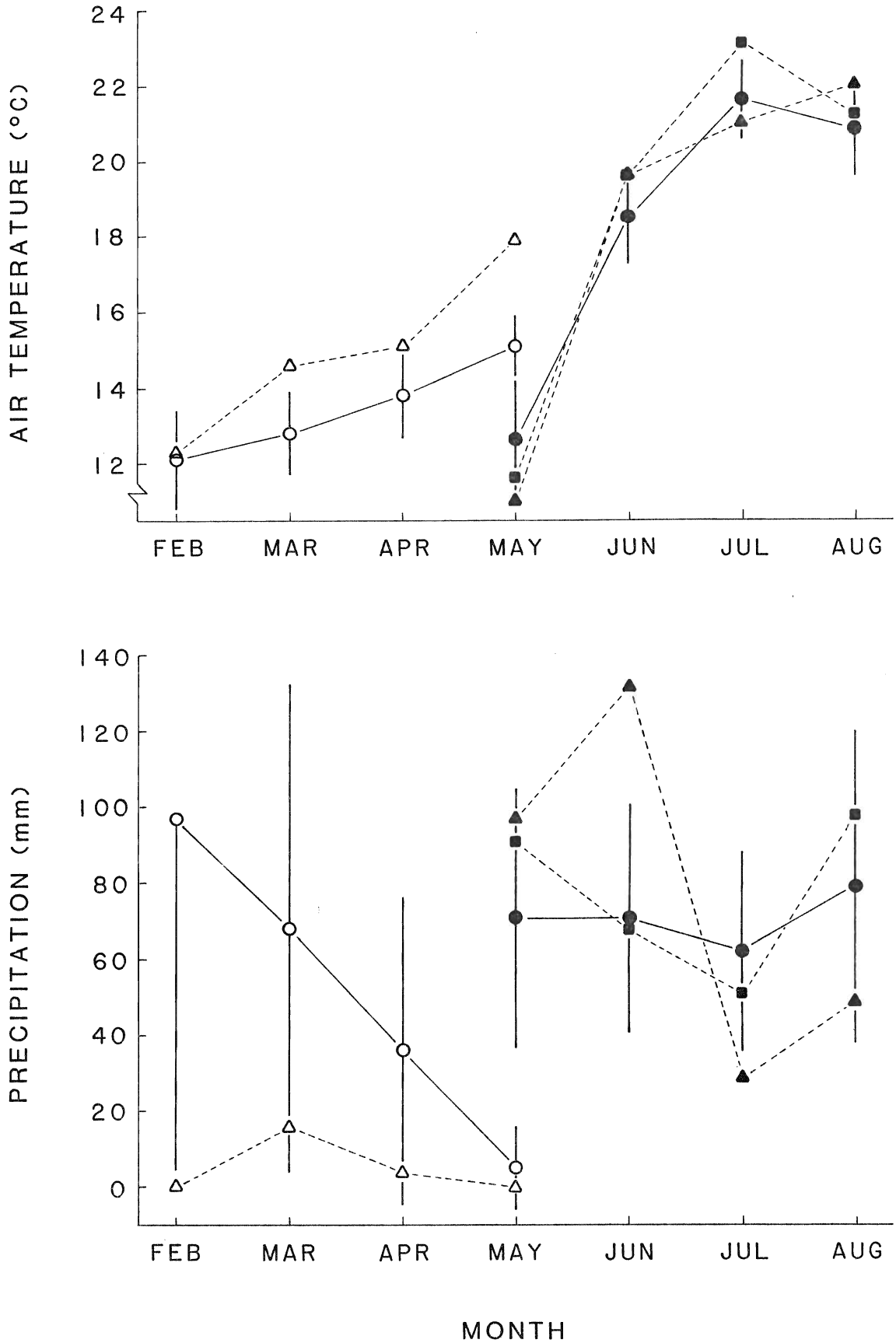

120
100
80
60
40
20
0
PRECIPITATION (mm)
J
F
M
A
M
J
J
A
S
O
N
D
MONTH

Figure 4. Mean monthly air temperature and precipitation calculated from data covering the period 1940-1982 in ONT (solid circles) and 1950-1983 in CAL (open circles). Vertical bars indicate ± 1 standard deviation. Broken lines indicate values of temperature and precipitation during survey months in ONT: 1983 (solid squares), 1984 (solid triangles); CAL: 1984 (open triangles). Air temperature and precipitation values during survey months were not included in the calculation of means.


AIR TEMPERATURE (°C)
24
22
20
18
16
14
12
FEB
MAR
APR
MAY
JUN
JUL
AUG
PRECIPITATION (mm)
140
120
100
80
60
40
20
0
FEB
MAR
APR
MAY
JUN
JUL
AUG
MONTH

high during June and low during July in 1984, was otherwise normal.

Morphometrics

Sexual dimorphism

For both the ONT and CAL samples MANOVA showed significant dimorphism between the sexes in skeletal characters and weight (ONT: Rao's $F = 3.211$, $df = 16$ and 33, $P < 0.01$; CAL: Rao's $F = 6.436$, $df = 16$ and 33, $P < 0.001$) and external characters and weight (ONT: Rao's $F = 5.962$, $df = 10$ and 39, $P < 0.001$; CAL: Rao's $F = 6.138$, $df = 10$ and 39, $P < 0.001$). Consequently, the sexes were treated separately in most subsequent analyses.

Seasonal variation in body weight

Observed changes in body weight are largely explained by seasonal variation in fat deposits (Dawson and Carey 1976; White and West 1977; Carey et al. 1978; Prescott 1983). In this study ONT and CAL birds were collected during the winter and spring of 1984, respectively, and hence interlocality variation in weight may be construed as variation in fat deposits rather than lean body weight. Partin (1933) demonstrated a seasonal variation in the weight of the House Finch that showed a February peak and November low in body weight, presumably reflecting seasonal variation in fat deposits. Chi-square analysis of fat score data in this study showed no significant difference in visible fat content of ONT and CAL individuals (Table 2). Thus interlocality differences in body weight represent variation in lean body weight.

Table 2. Frequency of visible fat categories of House Finches from ONT and CAL collected in 1984 during January-February and March, respectively. Comparisons were made with 2X2 contingency chi-square tests.

	Locality	Visible Fat Category			
		Nil	Light	Moderate	Heavy
Males	ONT	0	16	5	4
	CAL	4	13	8	0
		X^2 = 0.089[a], df = 1, P >> 0.05			
Females	ONT	0	16	9	0
	CAL	2	15	8	0
		X^2 = 0.089[a], df = 1, P >> 0.05			

[a] adjacent fat categories were combined (nil+light, moderate+heavy) to achieve acceptable expected frequencies.

Skeletal characters and weight

MANOVA showed highly significant interlocality differences in skeletal characters and weight of males (Rao's F = 4.911, df = 16 and 33, P < 0.001) and females (Rao's F = 3.631, df = 16 and 33, P < 0.001). It was therefore appropriate to proceed with univariate ANOVA on each separate character to explain the overall MANOVA significance.

Means and standard deviations of characters are given in Table 3. Significant variation was found in five characters of males and eight of females (Table 4). Both sexes vary significantly between locality in SKUL, PREL, TARL and CWEI in particular. Only females show differentiation in certain limb elements, which include HUML, ULNL, FEML, TIBL, whereas males have differentiatied in size of the pelvis (PELL). Of significant differences between means, bone dimensions are consistently smaller for birds of the ONT sample despite these individuals being significantly heavier (Table 3).

Because an omnibus MANOVA takes into account variation in all characters simultaneously, post hoc univariate ANOVAs of separate characters may not effectively explain the significant MANOVA effect. Characters that are invariant when considered univariately may contribute in a linear combination of intercorrelated characters producing the effect as detected by MANOVA. Hence, a truly multivariate examination of character variation was made using discriminant analysis.

Figure 5 shows frequency distributions of discriminant

Table 3. Statistics for morphological characters: mean (mm for linear dimensions, g for weight) , sample size (n), standard deviation.

	ONT		CAL	
Char.	Males	Females	Males	Females
SKUL	27.03(24)0.38	26.94(25)0.59	27.35(25)0.40	27.30(24)0.51
SKUW	14.29(25)0.22	14.19(25)0.32	14.21(25)0.14	14.11(25)0.25
SKUD	11.96(22)0.18	11.94(20)0.31	11.76(21)0.21	11.79(23)0.22
PREL	6.12(25)0.22	6.10(25)0.33	6.35(25)0.28	6.44(24)0.41
PREW	7.44(25)0.18[a]	7.41(25)0.16	7.33(25)0.24	7.33(25)0.28
PRED	4.70(25)0.18	4.63(23)0.20	4.68(22)0.18	4.65(21)0.17
MANL	18.75(25)0.37	18.81(23)0.50	18.97(23)0.50	18.82(25)0.46
MASL	5.69(25)0.25	5.70(23)0.29	5.78(23)0.37	5.73(25)0.27
MAND	3.42(24)0.11	3.43(25)0.11	3.46(25)0.15	3.48(25)0.11
CORL	16.58(25)0.47	16.59(25)0.51	16.59(25)0.38	16.52(25)0.38
STEL	21.56(25)0.72	21.31(25)0.74	21.42(24)0.48	21.11(25)0.63
KEED	10.44(25)0.47	10.19(25)0.45	10.54(24)0.33	9.95(25)0.37
HUML	17.62(25)0.42	17.47(25)0.39	17.78(25)0.37	17.70(21)0.28
ULNL	22.10(25)0.57	21.62(25)0.54	22.34(24)0.57	21.92(23)0.48
PELL	13.71(25)0.32	13.85(25)0.49	13.95(25)0.32	13.76(25)0.40
PELW	8.98(24)0.32	9.04(25)0.33	9.00(25)0.26	9.02(25)0.28
FEML	15.33(25)0.42	15.39(25)0.43	15.54(25)0.34	15.73(24)0.32
TIBL	25.13(23)0.61	25.20(25)0.68	25.43(24)0.63	25.60(25)0.63
TARL	17.14(25)0.45	17.09(23)0.58	17.44(25)0.43	17.59(24)0.51
BNL	8.53(25)0.30	8.56(25)0.31	8.50(25)0.32	8.58(25)0.38
BIL	10.17(25)0.43	10.06(25)0.28	10.44(25)0.40	10.41(25)0.33

BID	8.07(25)0.25	8.05(25)0.22	8.04(25)0.20	8.11(25)0.28
BWU	7.92(25)0.20	7.82(25)0.18	7.71(25)0.23	7.74(25)0.23
BWL	8.16(25)0.21	8.23(25)0.25	8.17(25)0.29	8.19(25)0.30[b]
WLP	77.48(25)1.60	75.80(25)1.53	78.32(25)1.66	75.72(25)1.77
WLS	64.82(25)1.24	62.86(25)1.11	65.08(25)1.46	63.56(25)1.70
TLL	60.21(24)2.18	58.87(25)1.51	60.56(25)1.99	59.56(25)1.86
TSL	16.41(25)0.55	16.50(25)0.69	16.54(25)0.56	16.45(25)0.49
WEI	21.90(25)1.26	22.12(25)1.35[c]	20.60(25)0.94	20.62(25)1.73
CWEI	2.80(25)0.05	2.81(25)0.06[d]	2.74(25)0.04	2.74(25)0.08

---

a These data were significantly skewed to the right (g_1 = 1.314, $P < 0.001$) and leptokurtic (g_2 = 2.282, $P < 0.05$).

b These data were significantly leptokurtic (g_2 = 1.937, $P < 0.05$).

c These data were significantly skewed to the right (g_1 = 1.062, $P < 0.05$).

d These data were significantly skewed to the right (g_1 = 0.931, $P < 0.05$).

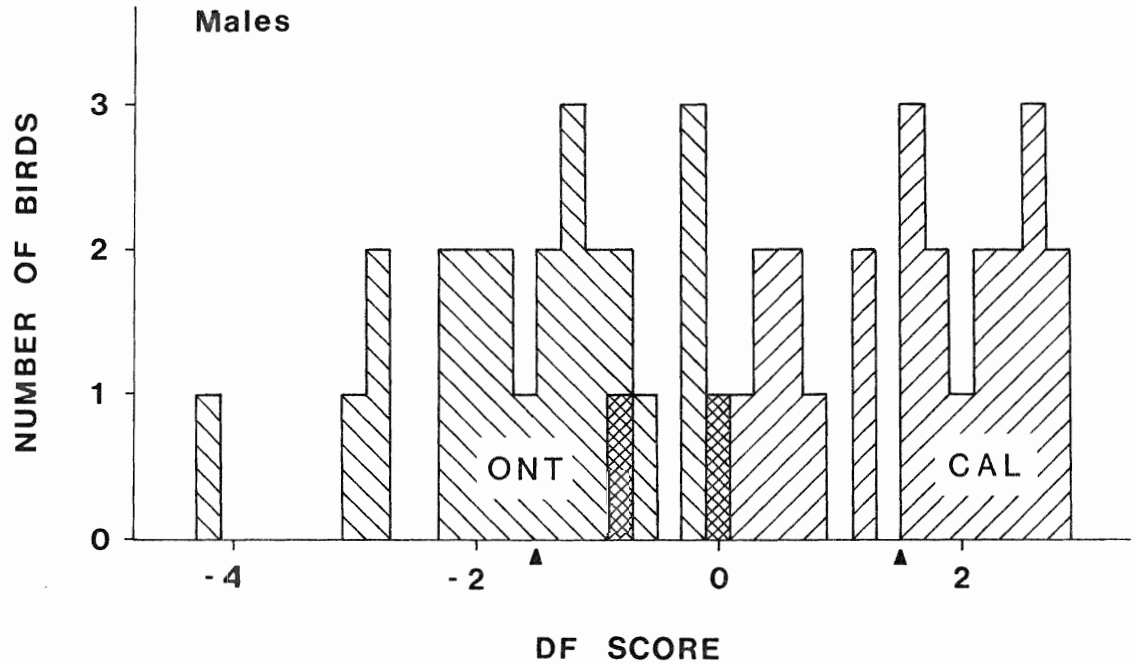
Table 4. Variation of skeletal characters and weight between ONT and CAL House Finches. Single-classification analysis of variance was used to compare character means.

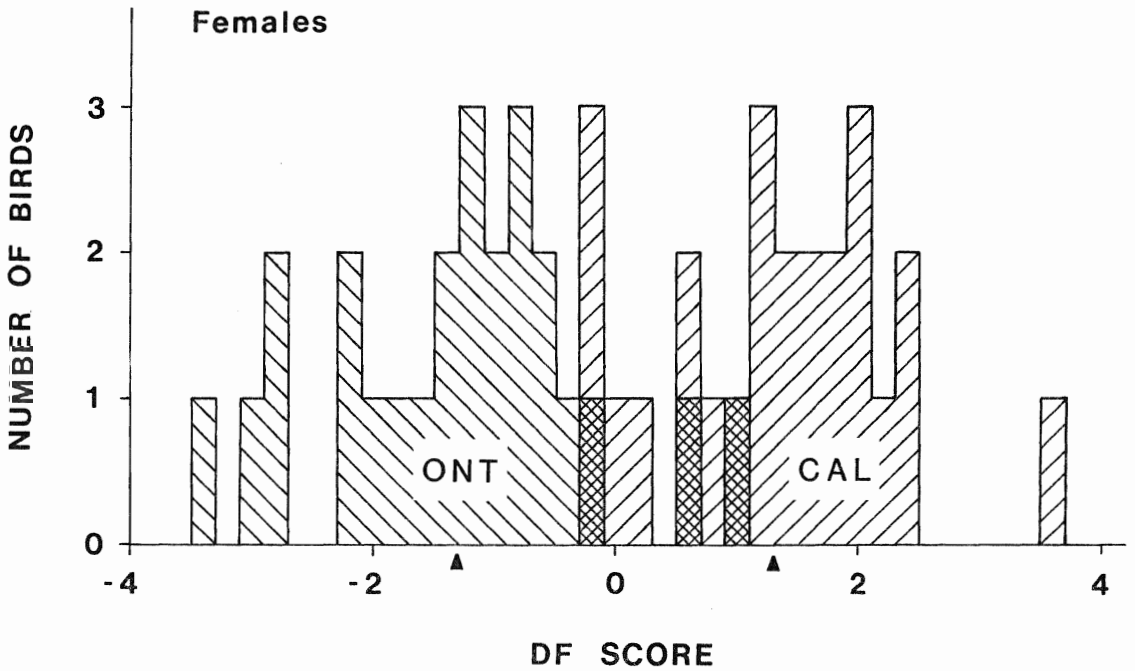
Character	F-ratio[a] Males	Females
SKUL	8.39 **	5.12 *
SKUW	2.52[b]	1.18
PREL	9.70 **	10.08 **
PREW	3.12	1.35[b]
MAND	1.23	2.10
CORL	0.01	0.34
STEL	0.73	1.03
KEED	0.73	3.90
HUML	2.06	4.87 *
ULNL	2.13	4.20 *
PELL	7.33 **	0.59
PELW	0.09	0.05
FEML	3.95	10.06 **
TIBL	2.78	4.71 *
TARL	5.85 *	10.21 **
CWEI	17.14 ***	12.29 ***

[a] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[b] Brown-Forsythe adjusted F for heterogeneous variance.

Figure 5. Distribution of discriminant function (DF) scores of populations of House Finches based on skeletal characters and weight. Overlap in histograms is shown by double-hatching. Triangles indicate group centroids.


Males
NUMBER OF BIRDS
3
2
1
0
ONT
CAL
-4
-2
0
2
DF SCORE


Females
NUMBER OF BIRDS
3
2
1
0
ONT
CAL
-4
-2
0
2
4
DF SCORE

function (DF) scores for males and females based on skeletal characters and cube root of weight. Of the grouped cases, 98.0% were classified correctly in males and 90.0% in females. Standardized discriminant function coefficients of the 16 characters used to achieve maximum separation are given in Table 5. The coefficients indicate the relative contribution of each character for discrimination; the largest coefficients, irrespective of sign, being the most important for distinguishing groups.

Samples of males separate maximally due primarily to interlocality variation of (in descending order of importance) KEED, STEL, CWEI, HUML, SKUL, FEML, TARL, CORL and SKUW. Samples of females were distinguished mainly on the basis of (in descending order of importance) CORL, TARL, SKUL, PREW, CWEI, PREL and TIBL. Of these, comparable numbers of positive and negative coefficients indicate a shape difference between localities. Based on group centroids (males: -1.512 (ONT), 1.512 (CAL); females: -1.300 (ONT), 1.300 (CAL)), individuals of the CAL samples have high values on the discriminant function, and thus, compared to ONT individuals, CAL males have relatively large SKUL, KEED, HUML, TARL and small SKUW, CORL, STEL, FEML and CWEI while CAL females have relatively large SKUL, PREL, TIBL, TARL and small PREW, CORL and CWEI. Of the characters used for discrimination, KEED of males and CORL of females were most important for distinguishing samples. Interestingly, KEED and CORL are statistically invariant between localities when examined univariately as are SKUW, CORL, STEL, HUML and FEML of males and

Table 5. Standardized discriminant function coefficients of skeletal characters and weight used to achieve maximum separation between ONT and CAL samples of House Finches.

Character	Discriminant function coefficient	
	Males	Females
SKUL	0.627	0.694
SKUW	-0.386	0.003
PREL	0.255	0.423
PREW	-0.251	-0.543
MAND	0.010	0.034
CORL	-0.419	-0.838
STEL	-1.009	-0.221
KEED	1.175	-0.102
HUML	0.641	0.126
ULNL	-0.141	-0.148
PELL	0.263	-0.049
PELW	-0.129	0.187
FEML	-0.589	-0.035
TIBL	0.176	0.369
TARL	0.431	0.772
CWEI	-0.846	-0.448

PREW of females illustrating the multivariate nature of morphological differences between localities, particularly in males.

The structure of covariation among the characters was assessed by extracting PCs with associated eigenvalues greater than one (1) from total correlation matrices of males and females. Correlations (or loadings) and communality (the sum of squared correlations over all PCs) of each character with the PCs are given in Table 6 for males and Table 7 for females. The PCs combined account for 69.0 and 73.1% of the total variation in male and female samples, respectively, and thus provide adequate summaries of the original data structure.

For both sexes all characters load substantially on PC I except SKUW, PREW of males, and CWEI of females. Only loadings of about 0.30 or greater were interpreted because they indicate that at least 9% of the variance in a character is explained by the respective component. Since character loadings on PC I are all of the same sign and mainly large, PC I may be interpreted as a multivariate measure of overall size (Jolicoeur and Mosimann 1960; Rao 1964; Schnell 1970; Blackith and Reyment 1971; Gibson et al. 1976).

PC II shows representation from SKUL, PREW, KEED, ULNL, TARL and CWEI. The characters PREL, MAND and STEL of males also load on PC II as do SKUW, HUML, FEML and TIBL of females. Of the characters that contribute primarily to PC II, only those associated with appendages (for males: ULNL and TARL; for females: HUML, ULNL, FEML, TIBL and TARL) load negatively.

Table 6. Loadings of skeletal characters and weight on the first four principal components of male House Finches.

	Principal component				
Character	I	II	III	IV	Communality
SKUL	0.635	0.436	-0.346	0.262	0.782
SKUW	0.178	0.112	0.353	0.826	0.851
PREL	0.321	0.519	-0.533	0.192	0.693
PREW	0.062	0.607	0.159	-0.261	0.464
MAND	0.429	0.650	-0.295	-0.219	0.741
CORL	0.784	-0.211	0.329	-0.135	0.785
STEL	0.529	0.457	0.359	-0.054	0.620
KEED	0.615	0.296	0.428	-0.083	0.657
HUML	0.850	-0.252	-0.006	-0.170	0.816
ULNL	0.856	-0.352	0.018	0.084	0.863
PELL	0.504	0.213	-0.408	0.073	0.471
PELW	0.462	-0.124	0.270	0.001	0.302
FEML	0.747	-0.255	-0.338	-0.175	0.768
TIBL	0.859	-0.268	-0.006	-0.032	0.811
TARL	0.738	-0.337	-0.188	0.167	0.721
CWEI	0.288	0.336	0.700	-0.032	0.687
Eigenvalue	5.85	2.22	1.94	1.03	
% variance explained	36.5	13.9	12.1	6.5	

Table 7. Loadings of skeletal characters and weight on the first four principal components of female House Finches.

	Principal component				
Character	I	II	III	IV	Communality
SKUL	0.701	0.311	-0.484	-0.133	0.840
SKUW	0.171	0.312	0.226	0.804	0.824
PREL	0.500	0.136	-0.727	-0.026	0.797
PREW	0.457	0.495	-0.372	-0.064	0.597
MAND	0.548	0.254	-0.566	0.083	0.692
CORL	0.868	0.172	0.189	0.073	0.823
STEL	0.638	0.282	0.376	-0.146	0.650
KEED	0.359	0.583	0.292	-0.060	0.558
HUML	0.829	-0.383	0.029	-0.008	0.833
ULNL	0.824	-0.336	0.057	0.249	0.857
PELL	0.571	0.146	0.369	-0.356	0.610
PELW	0.312	0.176	0.343	-0.330	0.355
FEML	0.807	-0.442	0.042	-0.155	0.872
TIBL	0.809	-0.328	0.133	0.120	0.794
TARL	0.800	-0.433	0.057	0.142	0.851
CWEI	0.232	0.786	0.257	0.116	0.751
Eigenvalue	6.35	2.39	1.88	1.07	
% variance explained	39.7	14.9	11.8	6.7	

PC II is a measure of shape variation and individuals with a large score on this component have relatively short limbs; recall that PC I represents absolute size.

PC III shows contribution from SKUL, PREL, KEED, STEL and PELL. Variation is also shown in SKUW, CORL, FEML and CWEI of males and PREW, MAND and PELW of females. Of these, most attributes of the skull covary negatively as do PELL and FEML of males. PC IV represents variation in SKUW, which in females covaries inversely with pelvis size (PELL and PELW).

Separate PCAs were carried out on each of the locality samples to determine if characters are similarly covariant between localities. For both sexes similar patterns of character covariation are evident on PC I and PC II (Appendices 7a-7d).

To determine if PCA ordination of cases in multivariate space resulted in two phenetically distinct groups, interlocality variation of component scores of the first three PCs was compared using t-tests (Table 8). Between sample differentiation of component scores was not significant for both sexes on PC I and males on PC II. Therefore, individuals from ONT have not differentiated in general size on PC I, nor shape on PC II in the case of males. Significant differences in shape are evident for females on PC II and both sexes on PC III. Thus, on PC II females of the ONT sample are significantly heavier, have larger skull and core parts and shorter appendages than CAL females. For PC III ONT males have significantly larger core parts (CORL, KEED) and weight, and smaller SKUL, PREL, PELL and FEML than CAL males. Females from the ONT sample also have significantly larger

Table 8. Variation of individual component scores between ONT and CAL House Finches for the first three principal components based on skeletal characters and weight. T-tests were used to test differences.

PC	Sex	Locality	Component score $\bar{x}$ (SD)	t[a]
I	Males	ONT	-0.253 (1.072)	-1.83
		CAL	0.253 (0.872)	
I	Females	ONT	-0.221 (1.092)	-1.59
		CAL	0.221 (0.864)	
II	Males	ONT	0.084 (0.941)	0.59
		CAL	-0.084 (1.068)	
II	Females	ONT	0.540 (0.858)	4.50***
		CAL	-0.540 (0.836)	
III	Males	ONT	0.591 (0.955)	5.15***
		CAL	-0.591 (0.635)	
III	Females	ONT	0.347 (0.960)	2.59*
		CAL	-0.347 (0.932)	

[a] *, $P < 0.05$; ***, $P < 0.001$.

core parts (STEL, PELL, PELW) and smaller skull attributes (SKUL, PREL, PREW, MAND) than CAL females (see Table 6 and 7).

Character variation within and between localities

Intralocality variation of characters is given in Table 9. Variances are homogeneous for all but two characters. Significantly greater variation is shown for SKUW of males of the ONT sample (Bartlett-Box $F = 4.364$, $P < 0.05$) and PREW of females of the CAL sample (Barlett-Box $F = 6.236$, $P < 0.05$).

Variance components, expressed as the percent fraction of the total variation for each character attributed only to variation between localities, are given in Table 10. The degree of differentiation is not homogeneous with respect to individual characters. Certain core characters of males (CORL, STEL, KEED, PELW) and females (CORL, PELL, PELW) show no apparent geographic variation whatsoever. Although SKUL, PREL, PELL and CWEI of males and PREL, FEML, TARL and CWEI of females have differentiatied substantially between localities, the mean percent variance component for each sex is similar.

External characters and weight

MANOVA showed statistically significant interlocality differences in external characters and weight of males (Rao's $F = 5.464$, df = 10 and 39, $P < 0.001$) and females (Rao's $F = 8.054$, df = 10 and 39, $P < 0.001$). Follow-up univariate ANOVAs on single characters revealed significant differences between localities in three characters of males (BIL, BWU, CWEI) and two characters of females (BIL, CWEI) (Table 11). Of these,

Table 9. Intralocality variance of skeletal characters and weight of House Finches from ONT and CAL.

	Intralocality variance			
	Males		Females	
Character	ONT	CAL	ONT	CAL
SKUL	0.145	0.159	0.346	0.258
SKUW	0.049	0.021	0.100	0.064
PREL	0.050	0.080	0.109	0.166
PREW	0.034	0.060	0.026	0.075
MAND	0.012	0.022	0.013	0.012
CORL	0.221	0.144	0.257	0.146
STEL	0.513	0.228	0.550	0.401
KEED	0.224	0.106	0.200	0.136
HUML	0.177	0.134	0.149	0.079
ULNL	0.330	0.329	0.294	0.229
PELL	0.099	0.104	0.237	0.157
PELW	0.009	0.065	0.110	0.076
FEML	0.173	0.117	0.185	0.100
TIBL	0.375	0.400	0.465	0.401
TARL	0.204	0.181	0.331	0.261
CWEI	0.003	0.002	0.003	0.006

Table 10. Variance components (%) of skeletal characters and weight between ONT and CAL House Finches.

Character	Variance component	
	Males	Females
SKUL	23.19	14.41
SKUW	5.68	0.73
PREL	25.80	27.07
PREW	7.89	1.36
MAND	1.16	4.55
CORL	0.00	0.00
STEL	0.00	0.13
KEED	0.00	10.59
HUML	4.07	14.53
ULNL	4.41	11.81
PELL	20.19	0.00
PELW	0.00	0.00
FEML	10.56	27.01
TIBL	7.05	12.92
TARS	16.23	28.16
CWEI	39.47	31.25
Mean percent variance component	10.36	11.53

Table 11. Variation of external characters and weight between ONT and CAL House Finches. Single-classification analysis of variance was used to compare character means.

Character	F-ratio[a] Males	Females
BNL	0.12	0.06
BIL	5.53 *	15.99 ***
BID	0.17	0.91
BWU	12.09 **	1.91
BWL	0.01	0.22
WLP	3.32	0.03
WLS	0.46	2.97[b]
TLL	0.34	2.05
TSL	0.64	0.06
CWEI	17.14 ***	12.29 ***

[a] *, P < 0.05; **, P < 0.01; ***, P < 0.001.

[b] Brown-Forsythe adjusted F for heterogeneous variance.

character means of the ONT samples are larger for CWEI and BWU but smaller for BIL (Table 3).

Separation of the samples in discriminant space was strong and classified correctly 90.0 and 94.0% of male and female cases, respectively. Standardized discriminant function coefficients of the 10 characters used to achieve maximum separation are given in Table 12. Samples of males and females were distinguished mainly on the basis of variation in (descending order of importance) BIL, BNL, CWEI, BWU and WLS. The bill character BID also contributed substantially to separate samples of males.

As for skeletal characters, the external characters that contributed most for discrimination show comparable numbers of positive and negative coefficients indicating interlocality variation in shape. Based on sample centroids (males: -1.160 (ONT), 1.160 (CAL); females: -1.408 (ONT), 1.408 (CAL)), birds of the CAL samples have high values on the discriminant function, and thus are distinguished from ONT individuals by being lighter, having smaller BNL, BWU and larger BIL and WLS. CAL males also have relatively larger BID than ONT individuals. Of external characters, BIL best distinguished samples by locality.

Character loadings on the first four PCs for males and the first three PCs for females are given in Table 13 and 14, respectively. For each sex PC I shows contribution from all characters except TSL, and in the case of males, BIL, and thus represents a general size factor.

Table 12. Standardized discriminant function coefficients of external characters and weight used to achieve maximum separation between ONT and CAL samples of House Finches.

Character	Discriminant function coefficient	
	Males	Females
BNL	-0.847	-1.454
BIL	1.137	1.846
BID	0.456	-0.055
BWU	-0.526	-0.324
BWL	0.275	0.030
WLP	0.216	0.036
WLS	0.336	0.493
TLL	0.125	0.075
TSL	-0.125	0.056
CWEI	-0.718	-0.459

Table 13. Loadings of external characters and weight on the first four principal components of male House Finches.

	Principal component				
Character	I	II	III	IV	Communality
BNL	0.421	0.522	0.608	-0.255	0.885
BIL	0.036	0.614	0.711	-0.016	0.884
BID	0.642	0.420	-0.049	0.084	0.598
BWU	0.613	0.405	-0.357	-0.071	0.672
BWL	0.574	0.221	-0.128	0.404	0.558
WLP	0.430	-0.710	0.356	0.111	0.828
WLS	0.670	-0.539	0.134	0.045	0.759
TLL	0.578	-0.687	0.120	-0.182	0.854
TSL	0.034	0.116	0.052	0.909	0.843
CWEI	0.543	0.318	-0.501	-0.253	0.711
Eigenvalue	2.56	2.42	1.43	1.18	
% variance explained	25.6	24.2	14.3	11.8	

Table 14. Loadings of external characters and weight on the first three principal components of female House Finches.

	Principal component			
Character	I	II	III	Communality
BNL	0.718	0.254	-0.427	0.762
BIL	0.615	0.359	-0.613	0.883
BID	0.563	0.539	-0.144	0.628
BWU	0.638	0.348	0.380	0.672
BWL	0.664	0.158	0.464	0.681
WLP	0.520	-0.719	0.127	0.803
WLS	0.614	-0.582	-0.183	0.748
TLL	0.527	-0.736	-0.197	0.859
TSL	0.194	0.403	0.078	0.206
CWEI	0.544	0.013	0.642	0.708
Eigenvalue	3.32	2.19	1.45	
% variance explained	33.2	21.9	14.5	

PC II shows representation from BIL, BID, BWU, WLP, WLS and TLL. For males BNL and CWEI also load on PC II as does TSL of females. Of these, only the wing and tail characters covary negatively.

PC III shows variation primarily in BNL, BIL, BWU, CWEI, and in BWL of females and WLP of males. Here the bill length characters covary inversely with bill width characters and CWEI of both sexes, and wing length of males. For males PC IV represents variation in bill width (BWL) and TSL.

A summary of interlocality component score comparisons is given in Table 15. T-tests revealed that phenetically distinct groups (localities) were summarized in component space only on PC III. Thus in relative terms, individuals of the ONT sample are significantly heavier and have wider and shorter bills than CAL individuals. Males of the ONT sample appear to also have a smaller winglength (see Table 13).

Character variation within and between localities

Significant interlocality heteroscedasticity was found in only WLS of females (Barlett-Box $F = 4.063$, $P < 0.05$), which is significantly more variable in CAL (Table 16). Between locality components of variance (Table 17) show no geographic variation in BNL, BID, BWL and TSL. For males WLS and TLL are not variable between localities, nor is WLP of females. Substantial differentiation is evident for BIL and CWEI of both sexes, and BWU of males, however, the mean percent variance component for each sex is similar.

Table 15. Variation of individual component scores between ONT and CAL House Finches for the first three principal components based on external characters and weight. T-tests were used to test differences.

PC	Sex	Locality	Component score $\bar{x}$ (SD)	t[a]
I	Males	ONT	0.150 (0.927)	1.06
		CAL	-0.150 (1.066)	
I	Females	ONT	-0.069 (0.784)	-0.48
		CAL	0.069 (1.190)	
II	Males	ONT	0.186 (1.000)	1.32
		CAL	-0.186 (0.985)	
II	Females	ONT	0.049 (0.959)	0.34
		CAL	-0.049 (1.057)	
III	Males	ONT	-0.510 (0.865)	-4.16***
		CAL	0.510 (0.867)	
III	Females	ONT	0.566 (0.802)	4.83***
		CAL	-0.566 (0.855)	

[a] ***, P < 0.001.

Table 16. Intralocality variance of external characters and weight of House Finches from ONT and CAL.

	Intralocality variance			
	Males		Females	
Character	ONT	CAL	ONT	CAL
BNL	0.090	0.101	0.096	0.146
BIL	0.184	0.160	0.081	0.111
BID	0.060	0.038	0.047	0.081
BWU	0.039	0.054	0.031	0.053
BWL	0.045	0.085	0.064	0.087
WLP	2.572	2.748	2.354	3.127
WLS	1.539	2.118	1.240	2.882
TLL	4.771	3.940	2.286	3.468
TSL	0.304	0.316	0.481	0.241
CWEI	0.003	0.002	0.003	0.006

Table 17. Variance components (%) of external characters and weight between ONT and CAL House Finches.

Character	Variance component	
	Males	Females
BNL	0.00	0.00
BIL	15.34	37.47
BID	0.00	0.00
BWU	30.70	3.46
BWL	0.00	0.00
WLP	8.48	0.00
WLS	0.00	7.31
TLL	0.00	4.01
TSL	0.00	0.00
CWEI	39.47	31.25
Mean percent variance component	9.40	8.35

Interlocality comparison of sexual dimorphism

Significant sexual dimorphism in skeletal characters is evident only in KEED, ULNL and FEML of CAL individuals, and ULNL of ONT individuals (Table 18). Of significant mean differences, only FEML of females is larger (Table 3). For external characters males have significantly larger WLP and WLS in both localities, and TLL in ONT (Table 19).

MANOVA among all samples (males and females from ONT and CAL) revealed highly significant dimorphism between the sexes (Rao's $F = 5.257$, $df = 48$ and 241.68, $P < 0.001$), though sexual dimorphism has already been determined for ONT and CAL samples separately. Discriminant analysis separated strongly sex on DF I and classified correctly 80.0% of cases. Figure 6 shows the distribution of DF scores of males and females on the first discriminant function, which explains 55.4% of the variation among samples.

Contributions of the skeletal characters and weight for sexual discrimination are given in Table 20. The sexes separate maximally primarily on the basis of (in descending order of importance) ULNL, TIBL, CORL, KEED and FEML. Based on sample centroids on DF I (males: 1.035 (ONT), 1.673 (CAL); females: -1.460 (ONT), -1.248 (CAL)), males are distinguished from females by having relatively larger KEED and ULNL and smaller CORL, FEML and TIBL. The sum of the products of character measurements and their respective unstandardized discriminant function coefficients plus the constant may be used to determine the score of individuals on the discriminant function.

Table 18. Variation of skeletal characters and weight between male and female House Finches from ONT and CAL. Single-classification analysis of variance was used to compare character means.

Character	F-ratio[a] ONT	CAL
SKUL	0.38[b]	0.17
SKUW	1.61	3.08[b]
PREL	0.08	0.80
PREW	0.54	0.00
MAND	0.23	0.30
CORL	0.00	0.53
STEL	1.54	3.59
KEED	3.68	33.53 ***
HUML	1.73	0.78
ULNL	9.15 **	7.18 *
PELL	1.50[b]	3.76
PELW	0.49	0.07
FEML	0.25	4.05 *
TIBL	0.12	0.85
TARL	0.12	1.35
CWEI	0.36	0.00[b]

[a] *, P < 0.05; **, P < 0.01; ***, P < 0.001.

[b] Brown-Forsythe adjusted F for heterogeneous variance.

Table 19. Variation of external characters and weight between male and female House Finches from ONT and CAL. Single-classification analysis of variance was used to compare character means.

Character	F-ratio[a] ONT	CAL
BNL	0.16	0.78
BIL	1.10	0.11
BID	0.13	1.03
BWU	3.18	0.34
BWL	1.07	0.08
WLP	14.32 ***	28.77 ***
WLS	34.56 ***	11.55 **
TLL	6.28 *	3.39
TSL	1.65	0.25
CWEI	0.36	0.00

[a] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Figure 6. Distribution of discriminant function (DF) scores of male and female House Finches based on skeletal characters and weight. Overlap in histograms is shown by double-hatching. Triangles indicate group centroids.

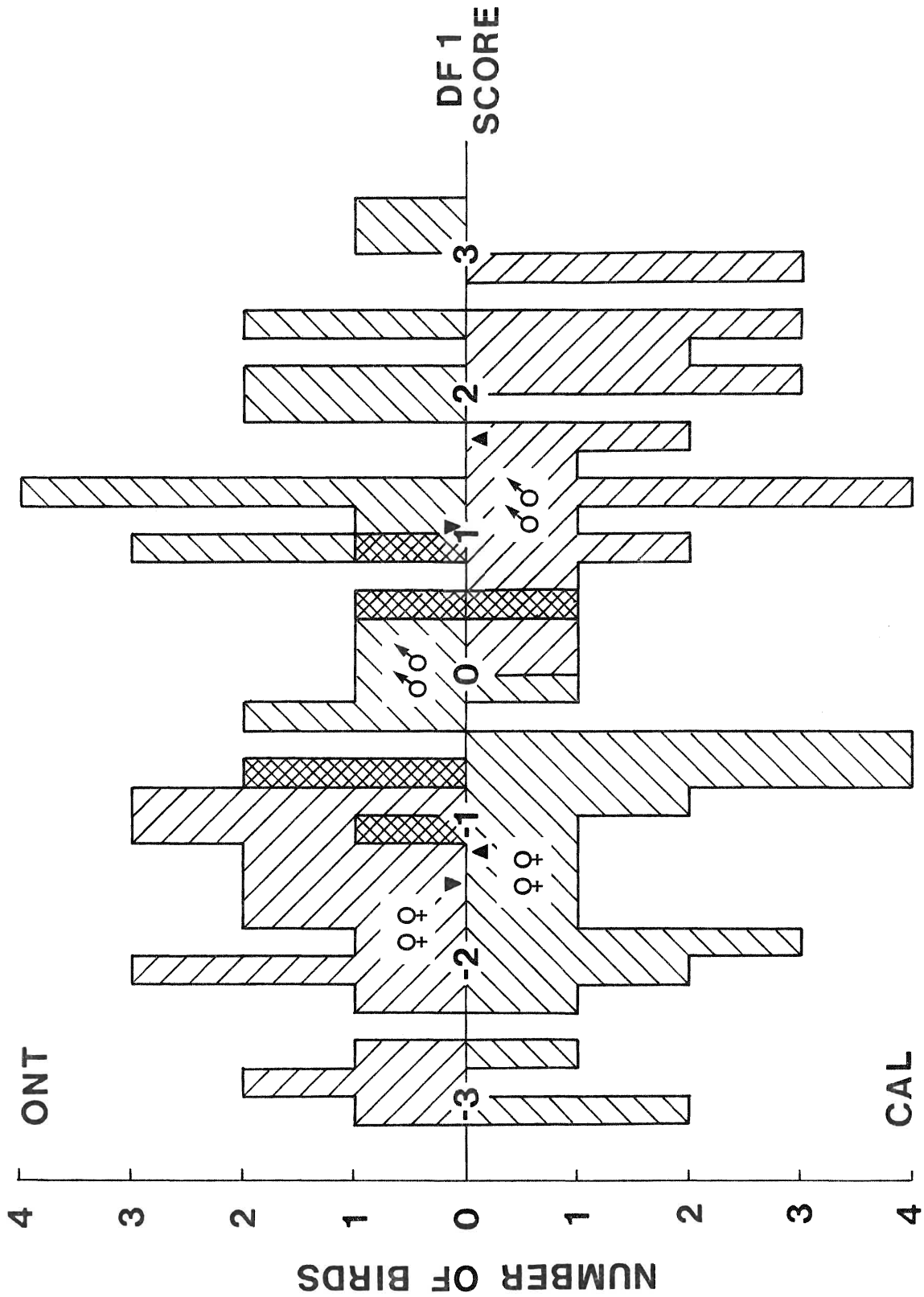

DF 1
SCORE
3
2
1
0
-1
-2
-3
ONT
CAL
4
3
2
1
0
1
2
3
4
NUMBER OF BIRDS

Table 20. Discriminant function coefficients of skeletal characters and weight used to achieve maximum separation between male and female House Finches on the first discriminant function (DF I). Localities were not pooled.

	DF I coefficients	
Character	Standardized	Unstandardized
SKUL	0.365	0.773
SKUW	-0.223	-0.922
PREL	-0.242	-0.769
PREW	0.216	0.976
MAND	-0.235	-1.937
CORL	-0.859	-1.962
STEL	0.090	0.138
KEED	0.848	2.094
HUML	0.055	0.151
ULNL	1.713	3.182
PELL	0.076	0.196
PELW	-0.229	-0.779
FEML	-0.598	-1.582
TIBL	-0.917	-1.446
TARL	0.340	0.670
CWEI	-0.382	-6.600
Constant		3.949

The difference of DF I scores between sex for each locality was used to compare the degree of sexual dimorphism between localities. Analysis by t-test showed no significant interlocality variation ($t = -1.02$, $df = 48$, $P >> 0.05$) in the mean difference of male and female DF I scores (ONT: $\bar{x} = 2.495$, $SD = 1.563$, $N = 25$; CAL: $\bar{x} = 2.921$, $SD = 1.399$, $N = 25$). Thus, disjunction differentiation of birds of the ONT sample has not affected the degree to which the sexes differ in morphology between localites.

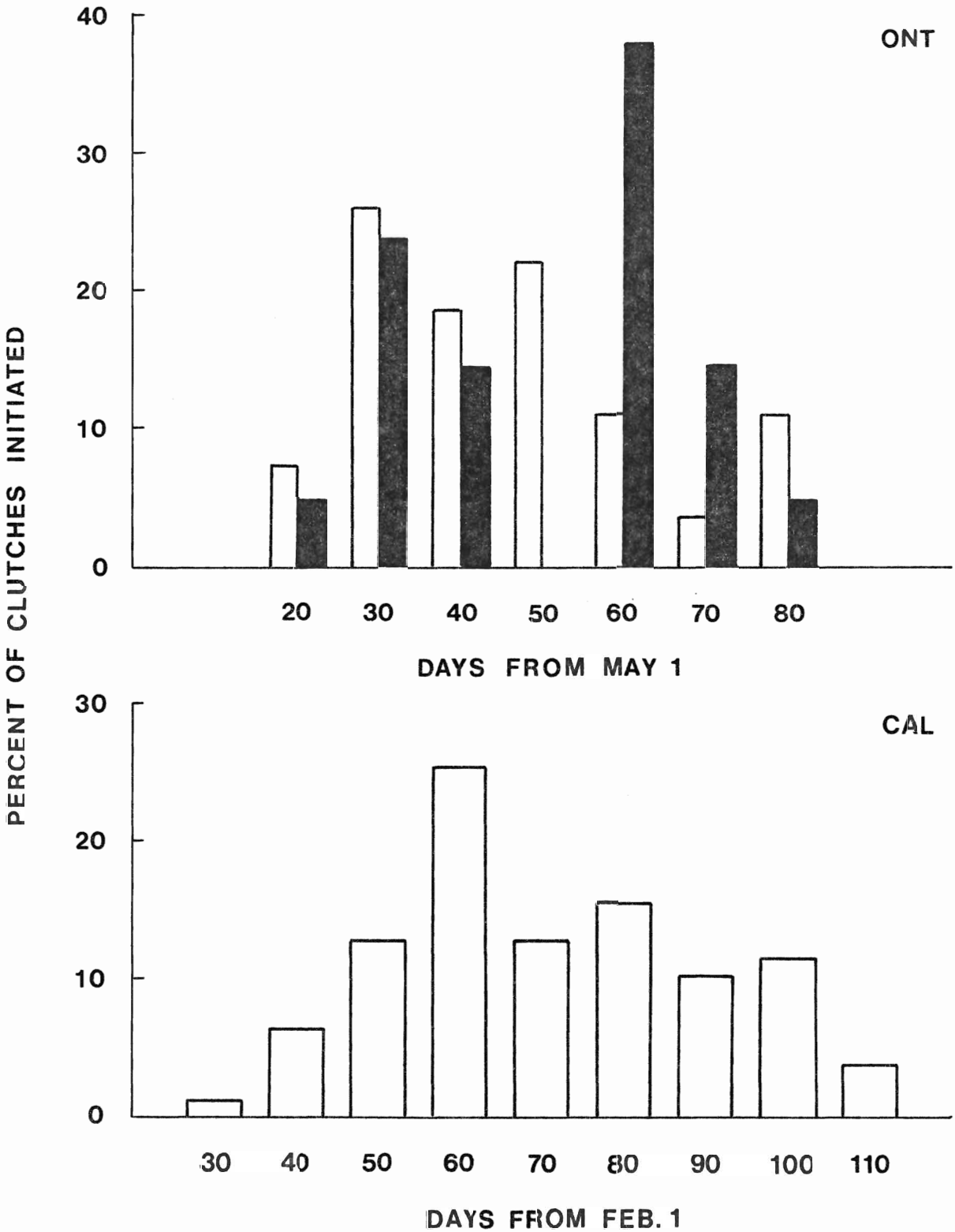
Nesting biology

The nesting season

The survey periods included the most intensive period of nesting in each population (Fig. 7). The earliest egg laying dates were 14 May for ONT in 1983, 17 May for ONT in 1984 and 27 February for CAL in 1984. There was no significant difference ($t = -0.971$, $df = 46$, $P > 0.05$) in mean clutch initiation date for ONT in 1983 ($\bar{x} = 41.48$, $SD = 16.99$, $N = 27$) and 1984 ($\bar{x} = 46.38$, $SD = 17.80$, $N = 21$).

House Finches usually produce a second clutch during a breeding season (Bergtold 1913; Gill and Lanyon 1965). Since breeding birds in this study were not individually marked, the proportion of second or replacement clutches is not known but is assumed to be comparable among the samples. Thus, any differences between first and second or replacement clutches would contribute to the 'error variance' in all samples.

Figure 7. Seasonal distribution of clutch initiation date in ONT in 1983 (open bars) and 1984 (solid bars), and CAL in 1984. Percent of clutches initiated were grouped into 10-day intervals (e.g. for CAL 30 = 21-30, 40 = 31-40 etc.). Sample size for ONT: 27 (1983), 21 (1984); CAL: 78 (1984).


ONT
40
30
20
10
0
20
30
40
50
60
70
80
DAYS FROM MAY 1
PERCENT OF CLUTCHES INITIATED
CAL
30
20
10
0
30
40
50
60
70
80
90
100
110
DAYS FROM FEB. 1

Clutch size and seasonal variation

Clutch size ranged from three to six eggs in ONT and three to five eggs in CAL (Table 21). Most nests contained either four or five eggs, though clutches of five were more frequently encountered in CAL. Chi-square analysis using only clutches of four and five revealed no significant difference in clutch size among the samples.

The relationship between the size of clutch and date of clutch initiation is presented in Fig. 8. A significant decrease in clutch size over the breeding season is evident in ONT in 1983 (Spearman rank coefficient of correlation, $r_s = -0.48$, $N = 23$, $P < 0.01$) and 1984 ($r_s = -0.47$, $N = 16$, $P < 0.05$), but not in CAL ($r_s = -0.13$, $N = 70$, $P >> 0.05$). Museum clutches from Los Angeles County showed no significant relationship between clutch size and date of collection for four and five egg clutches ($r_s = -0.02$, $N = 64$, $P >> 0.05$).

Egg size

Intralocality variation

To determine if reproductive effort involved a compromise between the number of eggs laid and egg size (i.e. an inverse relationship), egg characters were compared between and among clutch sizes (Table 22). Egg size was not influenced by the number of eggs laid except for egg length in the ONT sample in 1984 and egg weight, volume and breadth in the Oregon sample. Of these, mean egg length was smaller in clutches of four in the ONT sample and smallest in clutches of six in the Oregon sample. However, egg weight and breadth in clutches of five from Oregon

Table 21. Frequency of clutch sizes of House Finches from ONT during 1983 and 1984, and CAL during 1984. Comparison was made with a 3X2 contingency chi-square test.

Locality and year	N	Clutch size 3	4	5	6	$\bar{x}$
ONT 1983	24	1	12	11	0	4.42
ONT 1984	18	0	8	9	1	4.61
CAL 1984	81	2	34	45	0	4.53

$X^2 = 0.62$[a], df = 2, P > 0.05

[a] only clutches of four or five were used in analysis.

Figure 8. Seasonal variation of clutch size in ONT and CAL. Sample size for ONT: 23 (1983), 16 (1984); CAL: 70 (1984). Numerals indicate the number of clutches initiated on the same date.

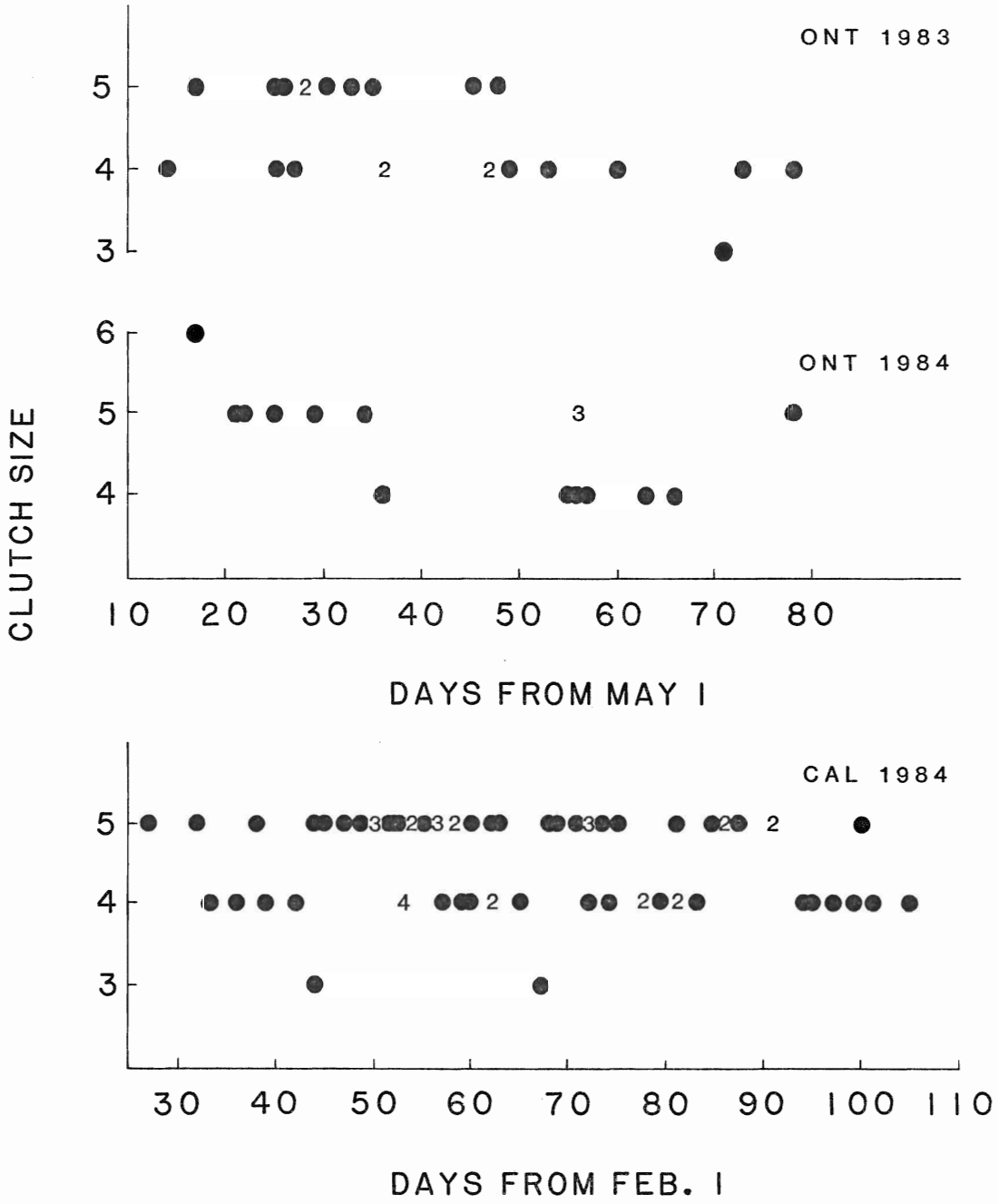

ONT 1983
5
4
3
6
ONT 1984
5
4
CLUTCH SIZE
10 20 30 40 50 60 70 80
DAYS FROM MAY 1
CAL 1984
5
4
3
30 40 50 60 70 80 90 100 110
DAYS FROM FEB. 1

Table 22. Variation of egg size among clutch sizes of House Finch eggs from ONT, CAL, Los Angeles County, California (L.A. Co.), and Oregon. T-tests and single-classification analyses of variance were used to test differences between and among clutch sizes, respectively.

Character, locality and year	Clutch size 4	5	6	t or F-ratio
Egg weight (g):				
ONT 1983	2.17(44)0.26[a]	2.14(44)0.19	-	0.55[b]
ONT 1984	2.12(28)0.24	2.23(38)0.21	-	-1.95
CAL 1984	2.00(96)0.23	1.98(146)0.19	-	0.57[b]
L.A. Co.	2.01(136)0.17	1.99(148)0.20	-	1.02
Oregon	2.05(12)0.17	2.15(55)0.16	1.98(18)0.15	8.08 ***
Egg volume (L*B*B; cm^3):				
ONT 1983	4.08(44)0.49	4.03(44)0.36	-	0.56[b]
ONT 1984	3.92(32)0.48	4.13(45)0.45	-	-0.98
CAL 1984	3.73(136)0.41	3.75(214)0.34	-	-0.37[b]
L.A. Co.	3.77(136)0.32	3.72(148)0.37	-	1.01
Oregon	3.85(12)0.32	4.04(55)0.30	3.72(18)0.29	8.02 ***
Egg length (mm):				
ONT 1983	19.60(44)0.98	19.74(44)0.90	-	-0.71
ONT 1984	19.00(32)1.08	19.77(45)1.08	-	-3.08 **
CAL 1984	19.03(136)0.94	19.04(214)0.97	-	-0.12
L.A. Co.	18.92(136)1.14	18.91(148)1.01	-	0.13
Oregon	19.83(12)1.03	19.77(55)0.81	19.00(18)0.82	6.12 **

Egg breadth (mm):

ONT 1983	14.39(44)0.65	14.27(44)0.42	-	1.09 [b]
ONT 1984	14.33(32)0.55	14.43(45)0.55	-	-0.79 [b]
CAL 1984	13.99(136)0.51	14.02(214)0.39	-	-0.65 [b]
L.A. Co.	14.10(136)0.41	14.02(148)0.50	-	1.52 [c]
Oregon	13.93(12)0.30	14.29(55)0.55	13.99(18)0.37	7.08 **

---

[a] mean, sample size (N), standard deviation.

[b] Separate variance estimate t-test.

[c] Brown-Forsythe adjusted F for heterogeneous variance.

were significantly larger than in clutches of four or six.

Mean egg weight per clutch showed no significant seasonal trend in ONT in 1983 (Pearson product moment coefficient of correlation, $r = 0.02$, $N = 24$, $P >> 0.05$, weight = 0.000date + 2.168g) and 1984 ($r = -0.18$, $N = 19$, $P >> 0.05$, weight = -0.003date + 2.343g), but increased significantly during the course of the breeding season in CAL ($r = 0.50$, $N = 62$, $P < 0.001$, weight = 0.005date + 1.595g) (Fig. 9). Similar results were found using the primary data rather than clutch means (ONT 1983: $r = 0.02$, $N = 92$, $P >> 0.005$, weight = 0.000date + 2.155g; ONT 1984: $r = -0.10$, $N = 77$, $P >> 0.05$, weight = -0.002date + 2.288; CAL: $r = 0.438$, $N = 263$, $P << 0.0001$, weight = 0.005date + 1.602). Mean egg weight showed no significant relationship with date of collection in museum eggs from Los Angeles County ($r = 0.21$, $N = 64$, $P > 0.05$, weight = 0.002date + 1.846). In the three samples more than 78% of the variation in mean egg weight in clutches of four and five is attributable to differences among clutches (ONT 1983: 80.59%, N = 19 clutches; ONT 1984: 78.40%, N = 15 clutches; CAL: 80.82%, N = 50 clutches). Similarly, in museum eggs from Los Angeles County 73.9% (N = 64 clutches) of the variation in egg weight is explained by differences among clutches.

Depending on the order in which they were laid, eggs varied differently in weight in four and five egg clutches (Fig. 10). There was a bias for heavier eggs to be laid later in four egg clutches and in five egg clutches of the ONT sample until the penultimate egg, however, there is no significant difference

Figure 9. Seasonal variation of mean egg weight per clutch in ONT and CAL. Sample size for ONT: 24 (1983), 19 (1984); CAL: 62 (1984). Lines were fitted to the data using least squares linear regression.

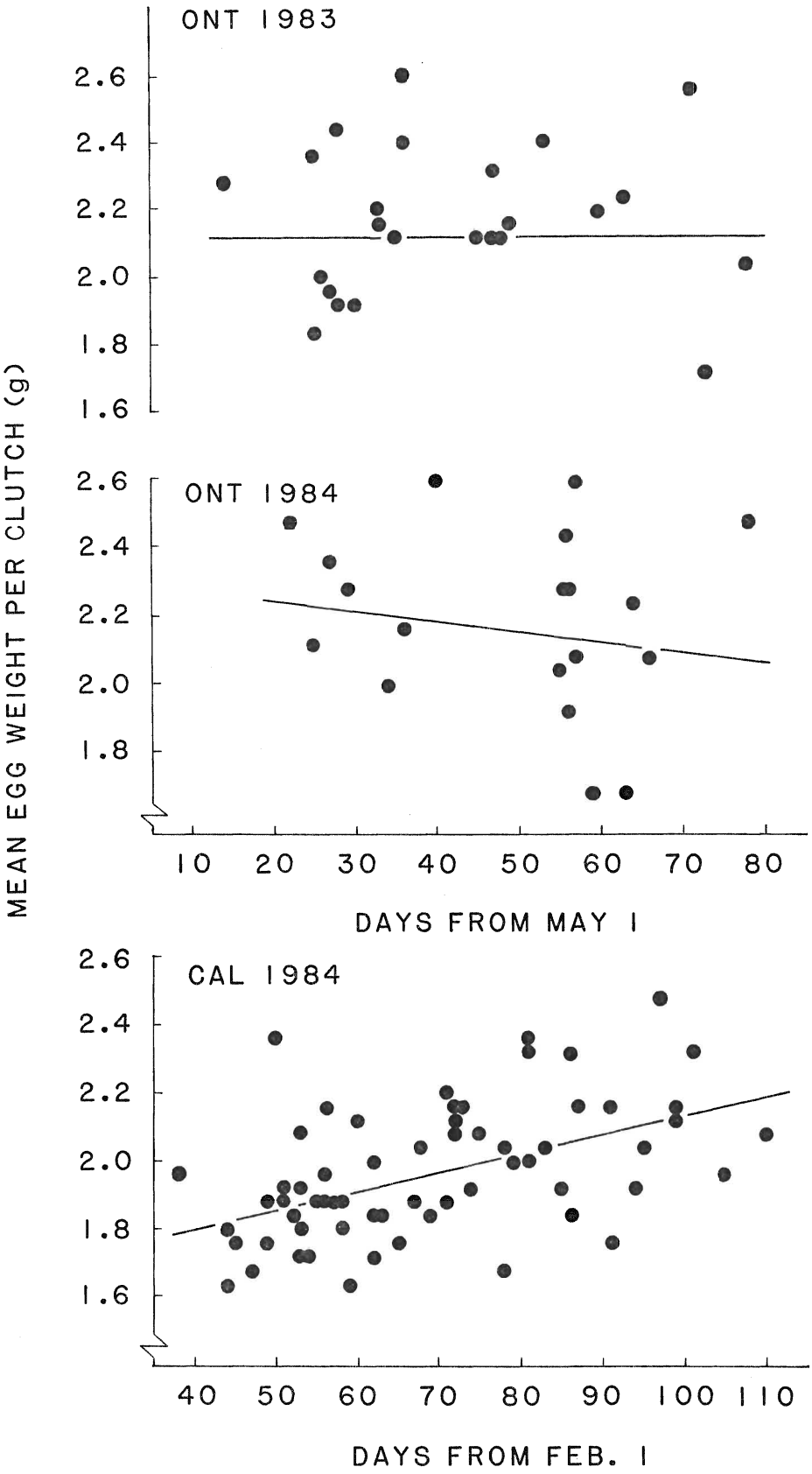
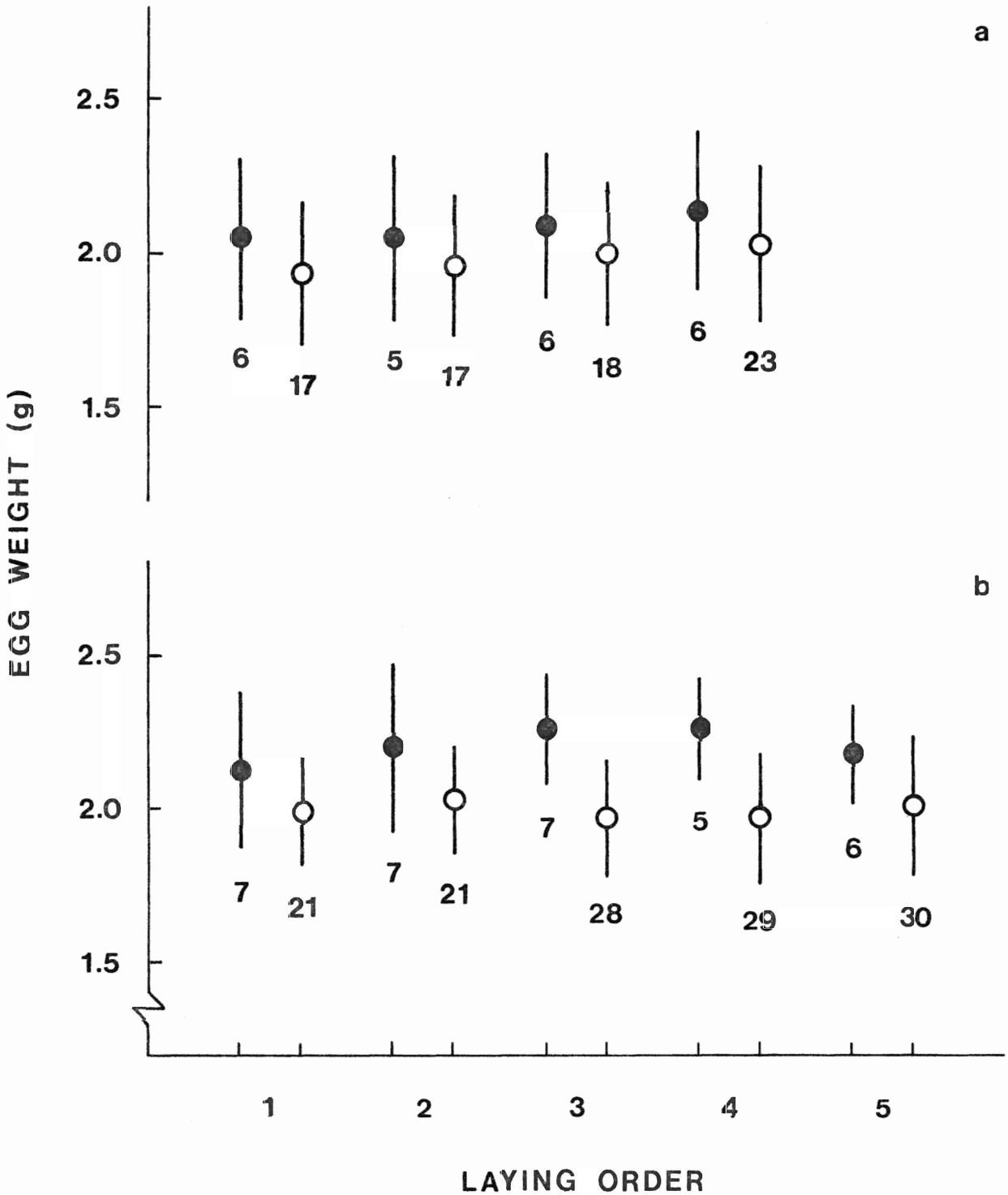

ONT 1983
ONT 1984
CAL 1984
MEAN EGG WEIGHT PER CLUTCH (g)
2.6
2.4
2.2
2.0
1.8
1.6
10 20 30 40 50 60 70 80
DAYS FROM MAY 1
40 50 60 70 80 90 100 110
DAYS FROM FEB. 1

Figure 10. Mean egg weight vs. order of laying for a. clutches of four and b. clutches of five in ONT (solid circles) and CAL (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes are shown below standard deviation bars.

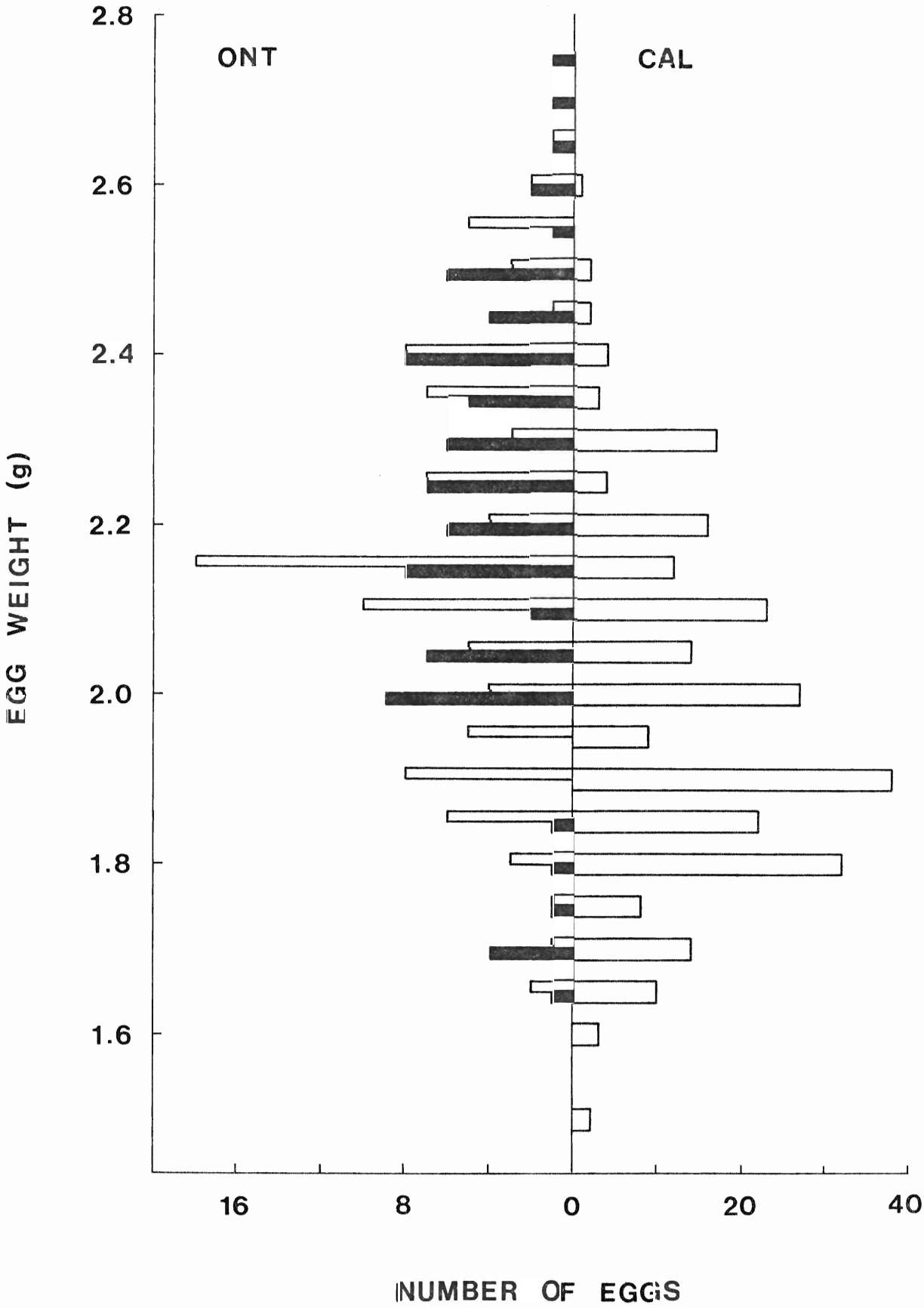

a
b
2.5
2.0
1.5
EGG WEIGHT (g)
6
17
5
17
6
18
6
23
7
21
7
21
7
28
5
29
6
30
1
2
3
4
5
LAYING ORDER

among means (for four egg clutches: ONT 1984: ANOVA F = 0.17, df = 3 and 19, P >> 0.05; CAL: ANOVA F = 0.64, df = 3 and 71, P >> 0.05; for five egg clutches: ONT 1984: ANOVA F = 0.52, df = 4 and 27, P >> 0.05; CAL: ANOVA F = 0.48, df = 4 and 124, P >> 0.05). However, differences within clutches may have been masked by the large variation in egg weight among clutches. Therefore, the effects of interclutch variation were removed by subtracting the mean egg weight of each clutch from individual egg weights within each clutch. Analysis of residual egg weights revealed that egg weight increased significantly with order of laying in clutches of four (ONT: ANOVA F = 5.35, df = 3 and 19, P < 0.01; CAL: ANOVA F = 6.62, df = 3 and 71, P < 0.001) but not in clutches of five (ONT: ANOVA F = 2.10, df = 4 and 27, P >> 0.05; CAL: ANOVA F = 2.30, df = 4 and 124, P >> 0.05).

Interlocality variation

Since there was no consistent pattern of significant differences in egg characters based on clutch size, the data were pooled regardless of clutch size for interlocality comparisons. Frequency distributions of egg weight for the three populations are presented in Fig. 11. Egg weight in ONT ranged from 1.65 - 2.65g in 1983, 1.65 - 2.75g in 1984, and in CAL from 1.50 - 2.60g. Since fresh egg weight for the ONT sample in 1983 was determined from measures of egg volume ($L * B^2$) the calculated egg weight range is 1.66 - 2.67g. However, individual egg weights were rounded to the nearest 0.05g for purposes of

Figure 11. Distribution of egg weight in ONT in 1983 (open bars) and 1984 (solid bars) and CAL in 1984. Sample size for ONT: 104 (1983), 82 (1984); CAL: 263 (1984).


ONT
CAL
2.8
2.6
2.4
2.2
2.0
1.8
1.6
EGG WEIGHT (g)
16
8
0
20
40
NUMBER OF EGGS

frequency distibution comparison, though not for statistical comparisons.

Differences in egg weight, volume, length and breadth are highly significant among the samples (Table 23). Of significant differences as determined by Scheffe's test, egg character means of the ONT samples are consistently larger than those of the California samples. Interestingly, eggs from the Oregon sample are intermediate in volume but indistinguishable from ONT eggs in terms of length, ONT 1983 eggs in terms of weight and Los Angeles County eggs in terms of breadth suggesting differences in egg compositon.

Egg characters did not vary significantly between years in ONT nor between samples from California despite atypical weather conditions particularly in CAL. Thus, in this study differences in egg size apparently were not influenced by proximate factors of ambient temperature and precipitation.

Incubation

Modal incubation time, from the laying of the last egg to its hatching, was 13 days for both locations and years in ONT (Table 24). To achieve acceptable expected values for Chi-square analysis, counts for ONT in 1983 and 1984 were combined and incubation periods other than 13 days were combined to produce a two-by-two contingency with cell counts: 18, 5, 15, 5. There is no significant difference in incubation time between localities.

Table 23. Variation of egg size of House Finch eggs from ONT, CAL, Los Angeles County, California (L.A. Co.), and Oregon. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different ($P > 0.05$) sets of means as determined by t-tests.

Character	Locality and year	$\bar{x}$ (N) SD	F-ratio[a]
Weight (g):	ONT 1984	2.22 (82) 0.24	
	ONT 1983	2.15 (104) 0.23	
	Oregon	2.10 (85) 0.17	33.51 ***
	L.A. Co.	2.00 (284) 0.19	
	CAL 1984	1.98 (263) 0.21	
Volume (L*B*B; cm^3):	ONT 1984	4.13 (103) 0.49	
	ONT 1983	4.06 (104) 0.43	
	Oregon	3.94 (85) 0.33	33.44 ***
	L.A. Co.	3.75 (284) 0.35	
	CAL 1984	3.73 (381) 0.37	
Length (mm):	ONT 1983	19.70 (104) 0.97	
	ONT 1984	19.61 (103) 1.18	
	Oregon	19.61 (85) 0.89	22.76 ***
	CAL 1984	19.00 (381) 0.97	
	L.A. Co.	18.92 (284) 1.07	
Breadth (mm):	ONT 1984	14.49 (103) 0.57	
	ONT 1983	14.33 (104) 0.54	
	Oregon	14.17 (85) 0.51	24.48 ***
	L.A. Co.	14.06 (284) 0.46	
	CAL 1984	13.99 (381) 0.45	

[a] Brown-Forsythe adjusted F for heterogeneous variance; ***, $P < 0.001$.

Table 24. Incubation periods of eggs of House Finches from ONT during 1983 and 1984, and CAL during 1984. Comparison was made with a 2X2 contingency chi-square test.

Locality and year	N	Incubation period (days) 12	13	14	15
ONT 1983	13	1	12	0	0
ONT 1984	10	1	6	2	1
CAL 1984	20	4	15	0	1

$X^2 = 0.064$[a], df = 1, P >> 0.05

[a] years in ONT and incubation periods other than 13 days were combined to achieve acceptable expected frequencies.

Nestling growth

The weight of newly hatched nestlings (day = 0) correlated with fresh egg weight in both localities (ONT in 1984: r_s = 0.78, N = 11, P < 0.01; CAL: r_s = 0.63, N = 29, P < 0.01). To determine if subsequent nestling growth was influenced by the number of young present in a nest, nestling size at hatching, three, six, nine and 13 days was compared among broods of three, four and five. Table 25 summarizes the results of comparisons using two-way factorial ANOVA for ONT data with year and brood size as main effects, and single-classification ANOVA among brood sizes for CAL data. Wing length was not available for analysis of nestlings at hatching, three or six days as primaries did not begin to emerge from the skin before seven days post hatching. There is no consistent pattern of significant differences in the growth of young among brood sizes for all characters and ages examined (see also Appendix 8). Consequently, the data were pooled regardless of brood size, though the 1983 and 1984 samples from ONT were analysed separately.

MANOVA showed significant differences in the size of nestlings at ages analysed among populations as well as in subsequent pairwise comparisons (Table 26). MANOVA on the original samples, which included identified outliers, yielded inflated Rao's F ratios among samples using nestlings of age three and nine days, and depressed ratios among samples using nestlings at hatching and six days (no outliers were found in samples of 13 day old nestlings). However, differences among the original samples remained highly significant (lowest Rao's F =

Table 25. Summary of results of two-way and single-classification analysis of variance of size of House Finch nestlings among broods of three, four and five using ONT and CAL data, respectively.

		Nestling age (days)									
		0		3		6		9		13	
Character	Effects[a]	ONT	CAL	ONT	CAL	ONT	CAL	ONT	CAL	ONT	CAL
Bill length	Year	NS	-	NS	-	NS	-	NS	-	NS	-
	Brood size	NS	NS	NS	*	*	NS	NS	NS	NS	NS
Bill depth	Year	*	-	**	-	NS	-	NS	-	NS	-
	Brood size	NS	*	NS	*	NS	NS	NS	NS	*	NS
Manus length	Year	NS	-	NS	-	**	-	NS	-	*	-
	Brood size	NS	NS	NS	*	NS	NS	**	*	NS	NS
Wing length	Year	-	-	-	-	-	-	NS	-	***	-
	Brood size	-	-	-	-	-	-	NS	**	NS	NS
Tarsometatarsus length	Year	NS	-	NS	-	NS	-	NS	-	*	-
	Brood size	NS	**	NS	NS	NS	NS	*	*	*	NS
Weight	Year	*	-	*	-	NS	-	NS	-	*	-
	Brood size	NS	**	NS	NS	*	NS	NS	**	NS	NS

[a] *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; NS, not significant.

Table 26. Multivariate analysis of variance of size of House Finch nestlings from ONT and CAL. Numerals in parentheses indicate sample size. Xs indicate samples used in respective analysis.

Nestling age (days)	Locality and Year: ONT 1983	ONT 1984	CAL 1984	df	Rao's F [a]
	(61)	(37)	(138)		
0	X	X	X	10, 458	16.35 ***
0	X	X		5, 92	5.85 ***
0	X		X	5, 193	17.65 ***
0		X	X	5, 169	23.17 ***
	(59)	(29)	(111)		
3	X	X	X	10, 384	7.98 ***
3	X	X		5, 82	6.27 ***
3	X		X	5, 164	4.88 ***
3		X	X	5, 134	14.00 ***
	(57)	(32)	(96)		
6	X	X	X	10, 356	18.23 ***
6	X	X		5, 83	9.03 ***
6	X		X	5, 147	28.10 ***
6		X	X	5, 122	14.03 ***
	(43)	(23)	(60)		
9	X	X	X	12, 236	13.27 ***
9	X	X		6, 59	2.93 *
9	X		X	6, 96	30.20 ***
9		X	X	6, 76	11.48 ***
	(29)	(11)	(60)		
13	X	X	X	12, 184	13.31 ***
13	X	X		6, 33	5.59 ***
13	X		X	6, 82	22.92 ***
13		X	X	6, 64	9.72 ***

[a] *, $P < 0.05$; ***, $P < 0.001$.

15.63, df = 10 and 462, P << 0.001), and thus cannot be attributed to the effects of deviant cases.

Growth curves for single characters of each population are presented in Fig. 12-17. Age related increase in weight from hatching (Fig. 12) is sigmoidal in shape, a pattern typical of most passerines (Ricklefs 1968). Nestlings of the ONT samples are consistently heavier than those of CAL throughout the entire growth period. ANOVA comparisons of weight at hatching, three, six, nine and 13 days revealed highly significant differences among the samples (Table 27). Unplanned comparisons of means showed that weight at hatching and three days differed significantly among all samples, while nestlings at six, nine and 13 days were statistically indistinguishable between years in ONT. The failure of weight to asymptote by day 14 in the ONT sample in 1984 is presumably attributed to low sample size (N = 7).

The growth of bill length (Fig. 13) and depth (Fig.14) is similar in that the rate of growth of both characters failed to decrease appreciably by day 14. Daily mean bill length and depth were consistently larger for ONT nestlings, though differences between localities are more pronounced for bill depth. Significant interlocality differences in mean bill length of nestlings at hatching, three and six days disappeared at nine and 13 days, however, nestlings of the ONT sample in 1984 remained significantly larger in terms of bill length than CAL individuals (Table 28).

Variation in bill depth among samples is highly significant (Table 29). Mean bill depth is significantly different among all samples for nestlings at hatching and three days, however, ONT samples were statistically invariant in terms of bill depth at six, nine and 13 days.

Manus growth (Fig. 15) is similar to that of body weight. Daily means are consistently larger for individuals of the ONT samples with the exception of nestlings at hatching. Of mean comparisons, interlocality variation is significant at all ages used except at hatching (Table 30). Non significantly different subsets of means were identified for ONT nestlings at three and nine days.

The daily growth of wing length was virtually linear (Fig. 16). Mean wing length of nestlings is larger in ONT than CAL throughout the growth period except on day 14. However, significant interlocality differences on day nine disappeared on day 13 (Table 31).

Increase in tarsometatarsus length was least variable among the populations although ONT nestlings generally show longer tarsi (Fig. 17). Significant interlocality differences occurred at hatching, three and six days but nestlings at nine and 13 days were statistically indistinguishable among samples (Table 32). Nestlings from ONT in 1983 were not significantly different in size from CAL individuals.

Figure 12. Mean increase of body weight of nestlings from hatching (0) to 14 days of age in ONT in 1983 (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes decreased during the growth period. Sample sizes for ONT: 62-18 (1983), 38-7 (1984); CAL: 139-48 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

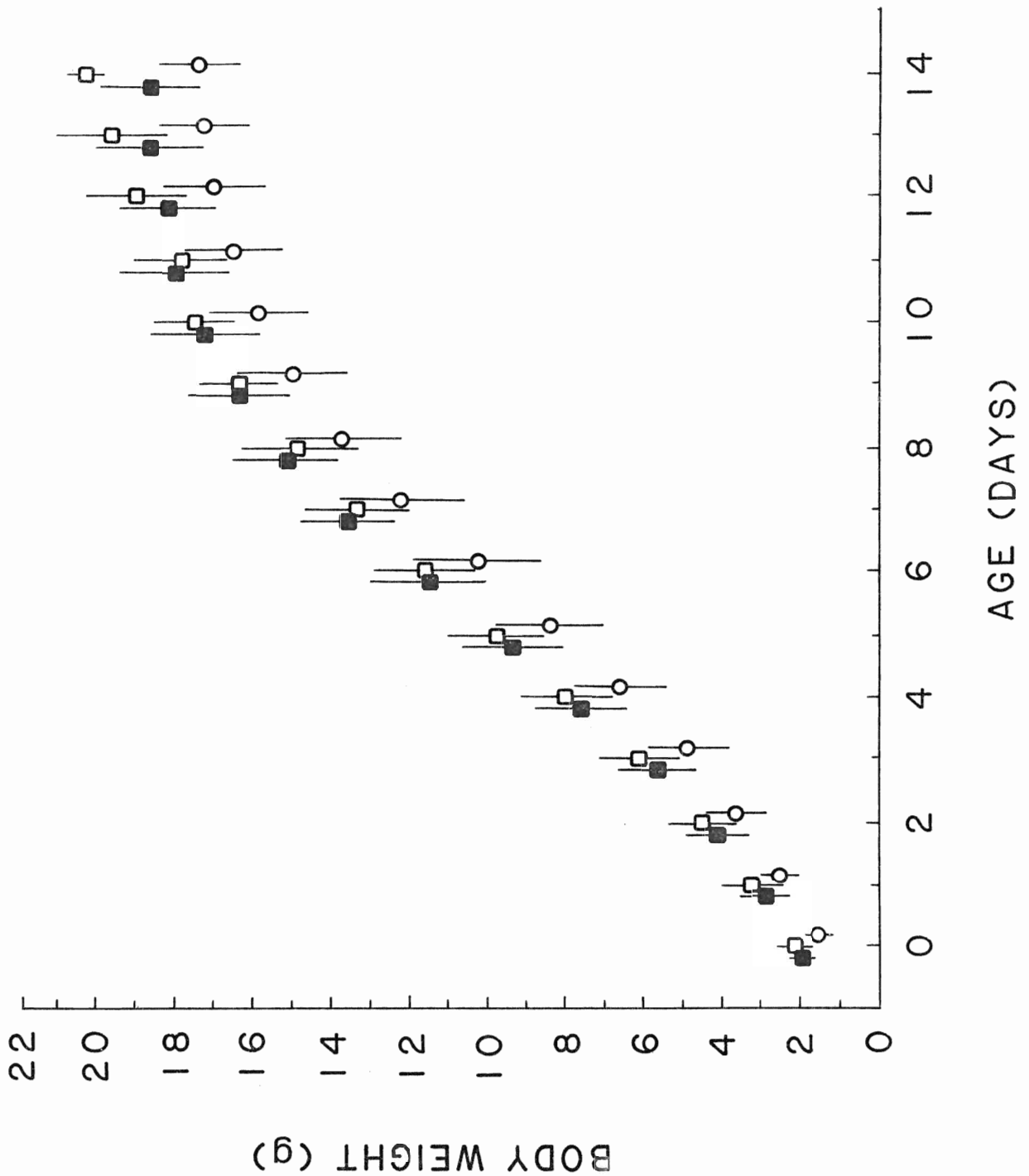

BODY WEIGHT (g)
0
2
4
6
8
10
12
14
16
18
20
22
AGE (DAYS)
0
2
4
6
8
10
12
14

Figure 13. Mean increase of bill length of nestlings from hatching (0) to 14 days of age in ONT in 1983 (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes decreased during the growth period. Sample sizes for ONT: 62-18 (1983), 37-7 (1984); CAL: 139-48 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

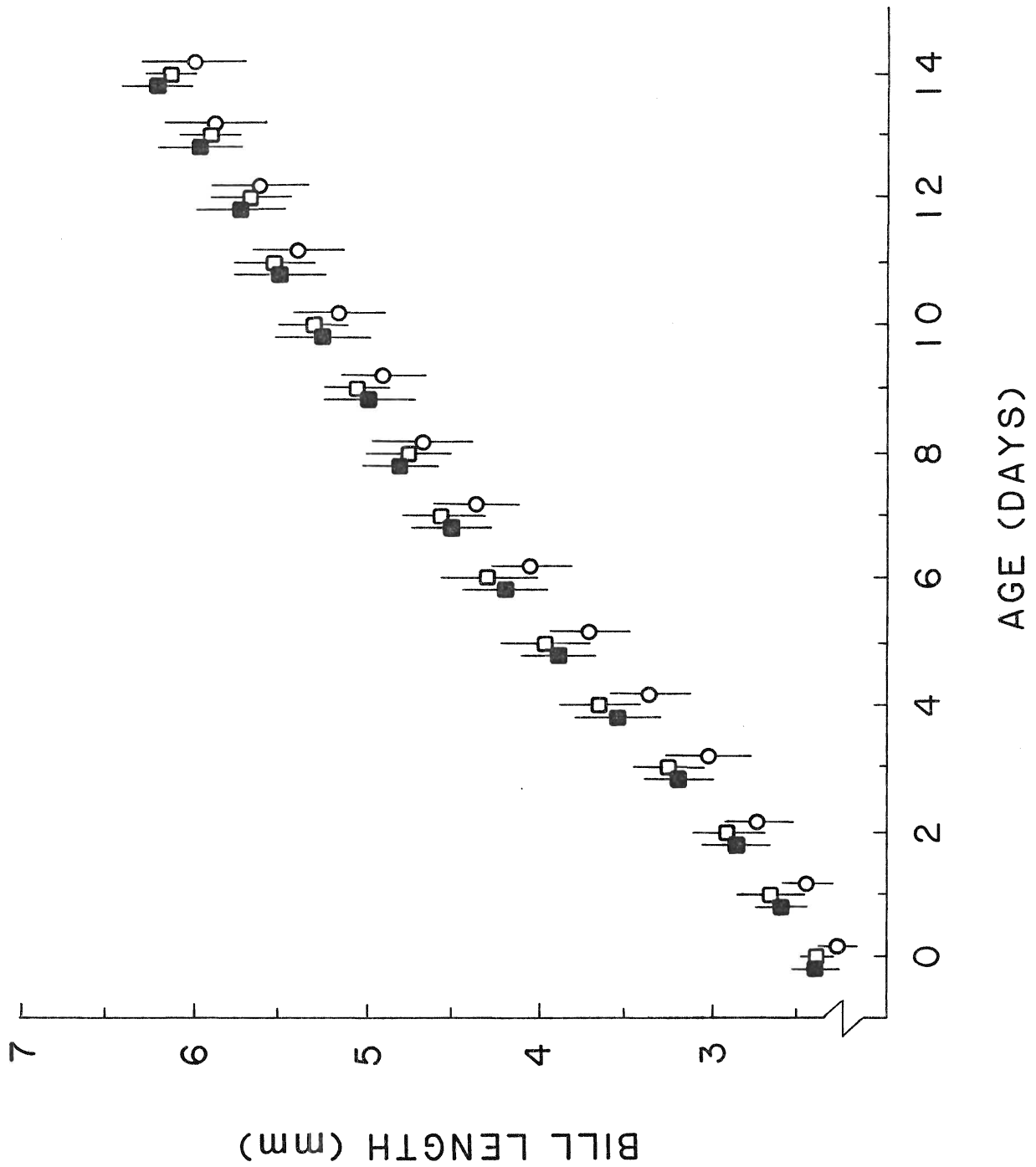

BILL LENGTH (mm)
7
6
5
4
3
AGE (DAYS)
0
2
4
6
8
10
12
14

Figure 14. Mean increase of bill depth of nestlings from hatching (0) to 14 days of age in ONT in 1983 (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical lines indicate ± 1 standard deviation. Sample sizes decreased during the growth period. Sample sizes for ONT: 62-18 (1983), 37-7 (1984); CAL: 139-48 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

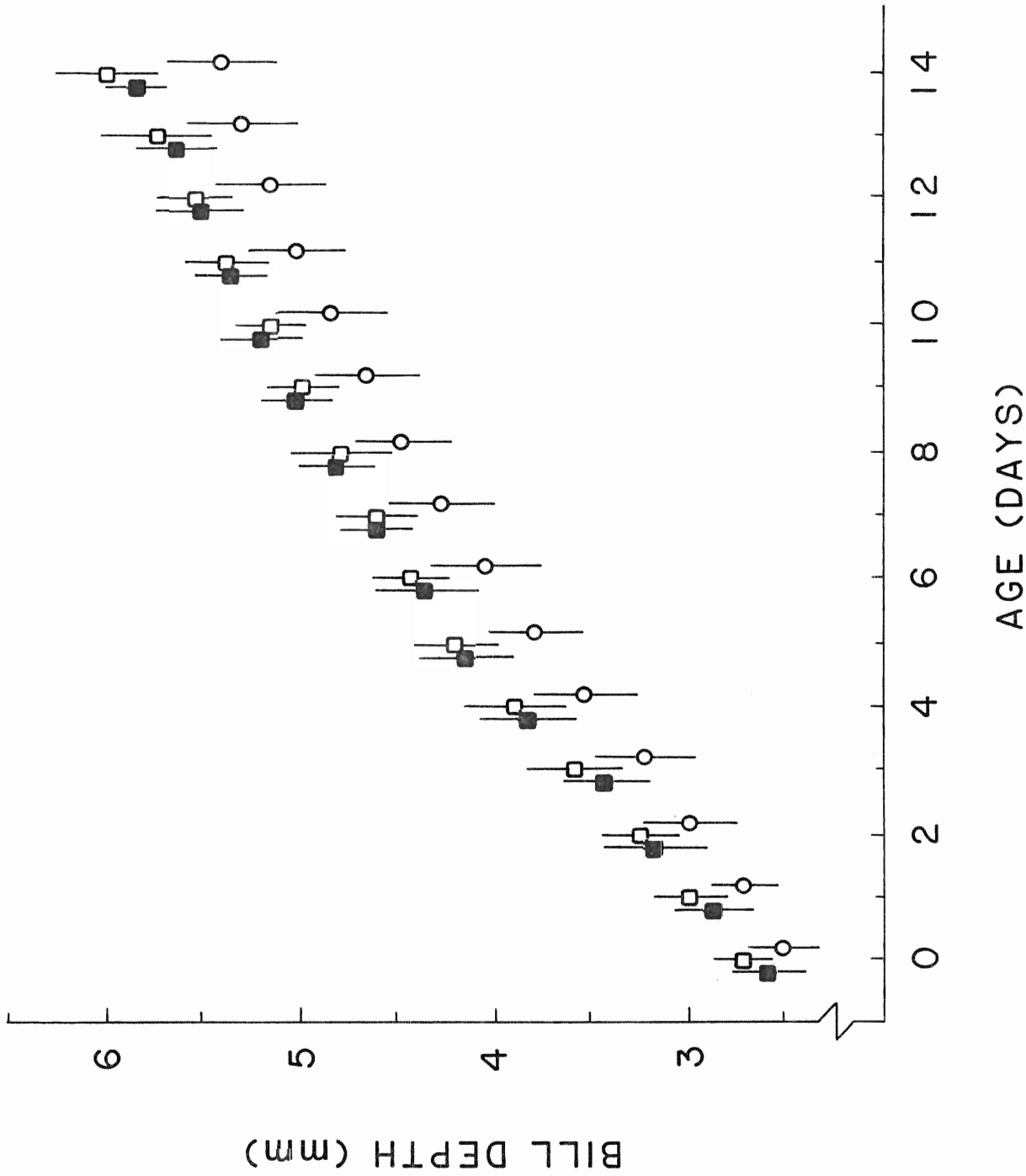

BILL DEPTH (mm)
6
5
4
3
0
2
4
6
8
10
12
14
AGE (DAYS)

Figure 15. Mean increase of manus length of nestlings from hatching (0) to 14 days of age in ONT (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes decreased during the growth period. Sample sizes for ONT: 62-18 (1983), 37-7 (1984); CAL: 139-48 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

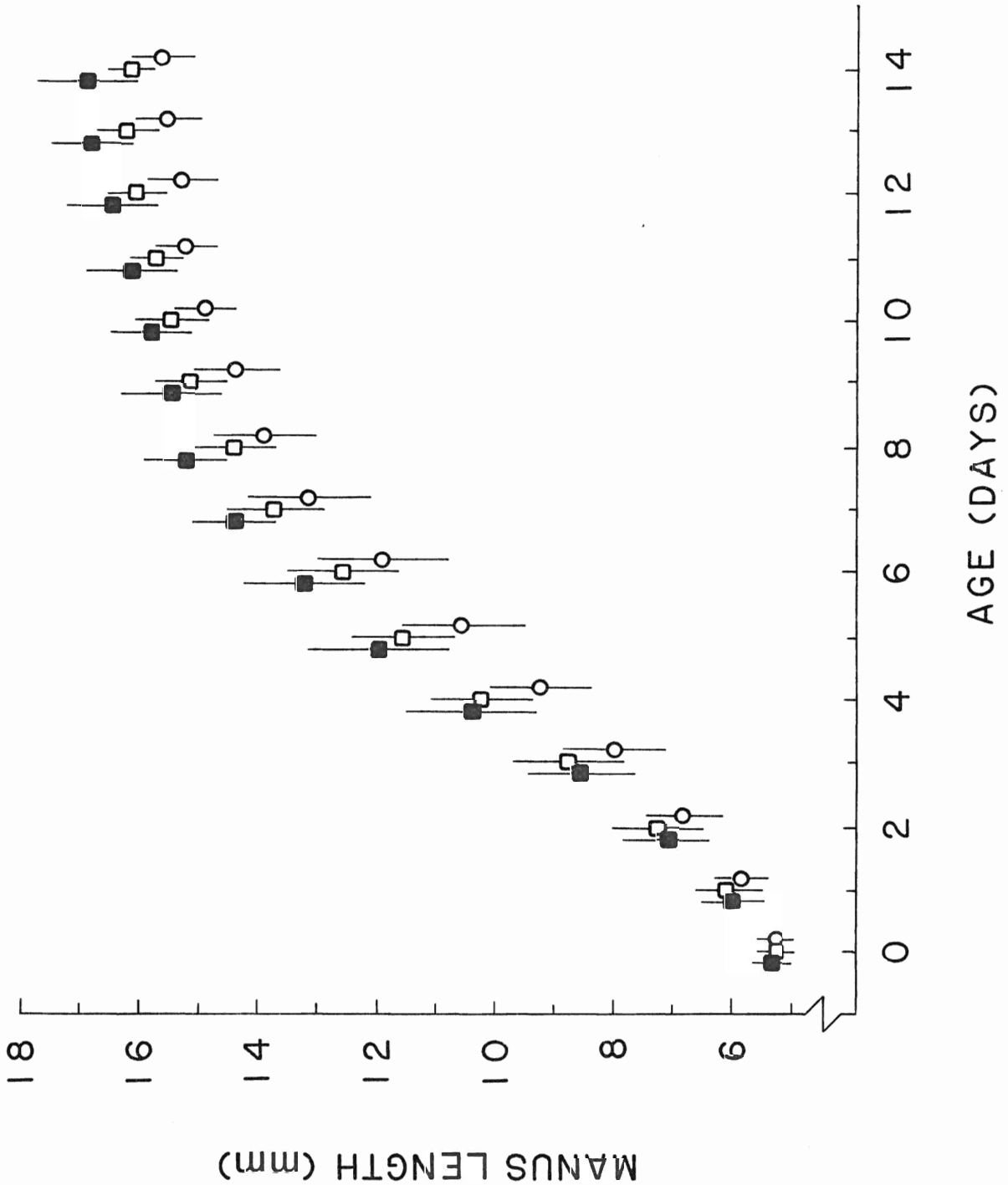

MANUS LENGTH (mm)
18
16
14
12
10
8
6
AGE (DAYS)
0
2
4
6
8
10
12
14

Figure 16. Mean increase of wing length of nestlings from hatching (0) to 14 days of age in ONT in 1983 (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes varied during the growth period. Sample sizes for ONT: 39-7 (1983), 20-1 (1984); CAL: 72-14 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

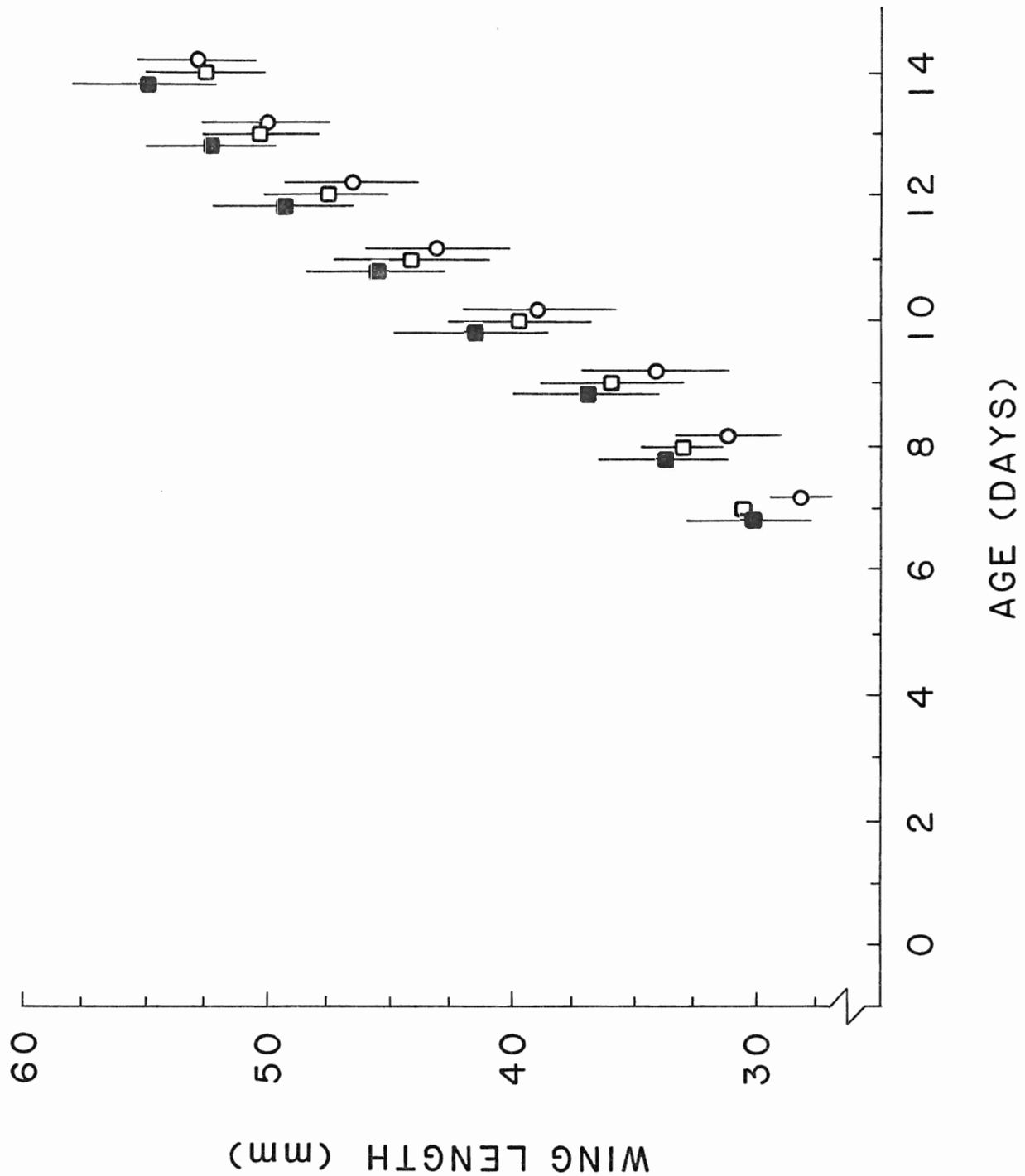

WING LENGTH (mm)
60
50
40
30
0
2
4
6
8
10
12
14
AGE (DAYS)

Figure 17. Mean increase of tarsometatarsus length of nestlings from hatching (0) to 14 days of age in ONT in 1983 (solid squares) and 1984 (open squares), and CAL in 1984 (open circles). Vertical bars indicate ± 1 standard deviation. Sample sizes decreased during the growth period. Sample sizes for ONT: 62-18 (1983), 37-7 (1984); CAL: 139-48 (Appendix 9). For convenience, sample means for ONT in 1983 and CAL are offset.

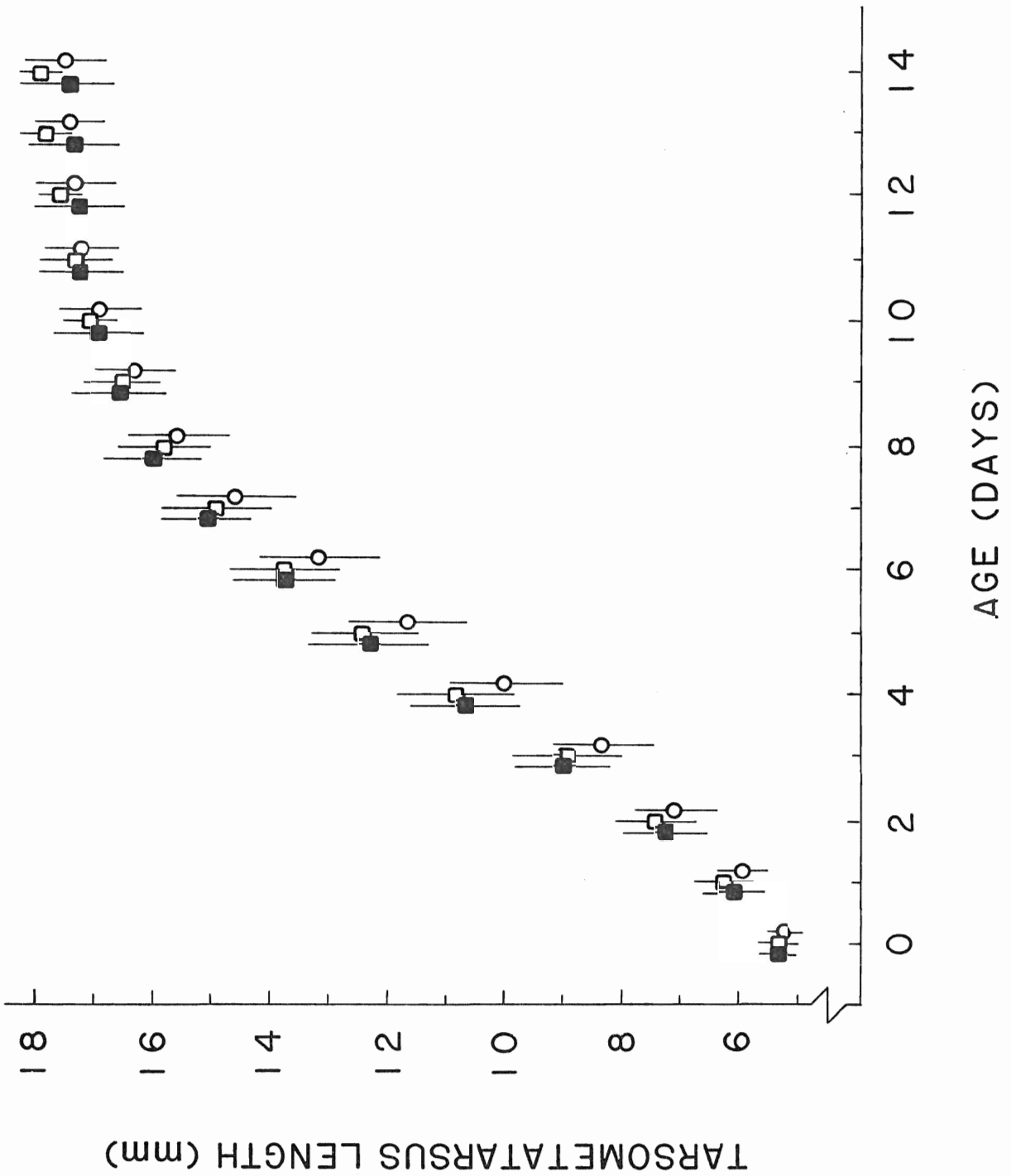

TARSOMETATARSUS LENGTH (mm)
18
16
14
12
10
8
6
0
2
4
6
8
10
12
14
AGE (DAYS)

Table 27. Variation of mean body weight of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio [a]
0	ONT 1984	2.10 (37) 0.43	[b]
	ONT 1983	1.87 (62) 0.32	14.31 ***
	CAL 1984	1.75 (139) 0.26	
3	ONT 1984	6.15 (31) 0.97	
	ONT 1983	5.62 (60) 0.93	26.94 ***
	CAL 1984	4.89 (116) 0.94	
6	ONT 1984	11.66 (33) 1.28	
	ONT 1983	11.54 (58) 1.44	17.94 ***
	CAL 1984	10.30 (99) 1.55	
9	ONT 1983	16.39 (44) 1.29	
	ONT 1984	16.35 (26) 0.92	19.78 ***
	CAL 1984	14.99 (64) 1.37	
13	ONT 1984	19.66 (11) 1.38	
	ONT 1983	18.70 (29) 1.31	25.74 ***
	CAL 1984	17.30 (60) 1.10	

[a] *** , P < 0.001.

[b] Brown-Forsythe adjusted F for heterogeneous variance.

Table 28. Variation of mean bill length of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio[a]
0	ONT 1983	2.40 (62) 0.11	44.55 ***
	ONT 1984	2.39 (37) 0.09	
	CAL 1984	2.27 (139) 0.10	
3	ONT 1984	3.24 (31) 0.21	17.55 ***
	ONT 1983	3.19 (60) 0.20	
	CAL 1984	3.02 (116) 0.24	
6	ONT 1984	4.29 (33) 0.27	17.08 ***
	ONT 1983	4.20 (58) 0.24	
	CAL 1984	4.03 (99) 0.25	
9	ONT 1984	5.05 (25) 0.18	5.25 **
	ONT 1983	4.98 (44) 0.26	
	CAL 1984	4.88 (64) 0.25	
13	ONT 1983	5.97 (29) 0.24	1.64
	ONT 1984	5.90 (11) 0.18	
	CAL 1984	5.86 (60) 0.29	

[a] **, P < 0.01; ***, P < 0.001.

Table 29. Variation of mean bill depth of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio[a]
0	ONT 1984	2.71 (37) 0.15	24.97 ***
	ONT 1983	2.59 (62) 0.16	
	CAL 1984	2.49 (139) 0.18	
3	ONT 1984	3.59 (31) 0.24	29.75 ***
	ONT 1983	3.42 (60) 0.22	
	CAL 1984	3.23 (116) 0.26	
6	ONT 1984	4.44 (33) 0.20	42.51 ***
	ONT 1983	4.36 (58) 0.26	
	CAL 1984	4.04 (99) 0.28	
9	ONT 1983	5.02 (44) 0.18	43.66 ***
	ONT 1984	4.98 (25) 0.18	
	CAL 1984	4.65 (64) 0.26	
13	ONT 1984	5.75 (11) 0.28	23.38 ***
	ONT 1983	5.64 (29) 0.20	
	CAL 1984	5.30 (60) 0.29	

[a] ***, P < 0.001.

Table 30. Variation of mean manus length of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio [a]
0	ONT 1983	5.35 (62) 0.35	0.21
	ONT 1984	5.32 (37) 0.30	
	CAL 1984	5.32 (139) 0.30	
3	ONT 1984	8.80 (31) 0.84	15.67 ***
	ONT 1983	8.58 (60) 0.87	
	CAL 1984	8.04 (116) 0.77	
6	ONT 1983	13.27 (58) 0.95	33.88 ***
	ONT 1984	12.61 (33) 0.86	
	CAL 1984	11.92 (99) 1.07	
9	ONT 1983	15.49 (43) 0.82	31.42 ***
	ONT 1984	15.12 (25) 0.57	
	CAL 1984	14.39 (64) 0.71	
13	ONT 1983	16.77 (29) 0.66	50.68 ***
	ONT 1984	16.23 (11) 0.51	
	CAL 1984	15.52 (60) 0.51	

[a] ***, P < 0.001.

Table 31. Variation of mean wing length of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio [a]
9	ONT 1983	36.84 (44) 3.00	11.64 ***
	ONT 1984	35.98 (24) 2.80	
	CAL 1984	34.16 (62) 2.88	
13	ONT 1983	52.34 (29) 2.54	7.63 ***
	ONT 1984	50.23 (11) 2.33	
	CAL 1984	50.13 (60) 2.61	

[a] ***, P < 0.001.

Table 32. Variation of mean tarsometatarsus length of nestling House Finches from ONT and CAL. Single-classification analysis of variance was used to test differences. Vertical bars indicate non-significantly different (P > 0.05) sets of means as determined by Scheffe's test.

Nestling age (days)	Locality and year	$\bar{x}$ (N) SD	F-ratio [a]
0	ONT 1983	5.39 (62) 0.28	4.21 *
	ONT 1984	5.38 (37) 0.35	
	CAL 1984	5.28 (139) 0.29	
3	ONT 1983	8.99 (60) 0.81	13.06 ***
	ONT 1984	8.96 (31) 0.88	
	CAL 1984	8.39 (116) 0.81	
6	ONT 1984	13.74 (33) 0.93	8.97 ***
	ONT 1983	13.73 (58) 0.86	
	CAL 1984	13.15 (99) 1.00	
9	ONT 1984	16.53 (25) 0.59	1.56
	ONT 1983	16.52 (44) 0.77	
	CAL 1984	16.32 (64) 0.65	
13	ONT 1984	17.81 (11) 0.36	2.77
	CAL 1984	17.37 (60) 0.60	
	ONT 1983	17.34 (29) 0.68	

[a] *, P < 0.05; ***, P < 0.001.

DISCUSSION

Morphometrics

House Finches of the introduced population (ONT) have undergone a limited amount of differentiation from native stock since their introduction to the eastern United States about 44 years ago. Of the 25 characters used in this study, analysis of variance revealed significant interlocality variation in only seven characters of males and nine of females. The sexes demonstrated different patterns of character variation; females showed differentiation in more limb elements than males. It is noteworthy that among skeletal attributes showing significant interlocality variation, character means were consistently smaller for individuals of the ONT sample.

Discriminant analysis, which considers variation in all characters simultaneously, distinguished samples on the basis of interlocality variation in the proportioning of body parts. Discrimination between populations was based on different sets of skeletal attributes from across the skeletal suite for each sex, though certain extremities were smaller relative to weight in birds of the ONT sample. Patterns of interlocality covariation of external characters showed consensus between the sexes. Birds in ONT were distinguished from CAL individuals by having shorter and wider bills, and narrower wings relative to body weight.

Principal components analysis of total correlation matrices yielded a set of independent constructs, which revealed underlying patterns of character covariation. Phenetically distinct groups (localities) were identified only on

size-independent components of variation (PC II and PC III). For skeletal characters PC II, which showed representation from certain skull attributes, a body core character, weight, and all limb characters, varied significantly between localities only in females. PC III described variation in certain skull attributes, certain body core parts and in males, weight. Patterns of character covariation on PC III were different between the sexes. For external characters significant variation between localities was revealed only on PC III, which explained variation primarily in bill dimensions and weight.

Previous studies have assessed univariately variation of external characters of native and introduced House Finches. Aldrich and Weske (1978) noted little differentiation between samples of House Finches from eastern and western United States, and found that birds in the east possessed significantly shorter tarsi and toes than individuals from California. Aldrich (1982) found that compared to birds from southern California, birds in the northeast were significantly larger in terms of culmen length and height of maxilla, and significantly smaller in terms of length of middle toe and in males winglength and tarsus length.

My data showed that small tarsus length (TARL) also was characteristic of the population in ONT, though no interlocality differentiation was found in terms of bill depth (BLD or MAND) or winglength (WLP). Furthermore, bill length (both BIL and PREL) was significantly smaller for ONT individuals, which is contrary to Aldrich's (1982) findings for the eastern population.

The limited scale of differentiation demonstrated by House Finches of the ONT sample is interesting given what has been found for recently established populations of other species. The North American populations of the House Sparrow, which were introduced from Europe during the period 1852-1860, showed significant differentiation among all of 16 skeletal (Johnston and Selander 1971) and five external (Selander and Johnston 1967; Johnston and Selander 1973) characters. Similarly, all five external characters were found to be geographically variable among South American populations of House Sparrows, which were introduced to Buenos Aires, Argentina in 1870 (Johnston and Selander 1973). New Zealand populations of the same species, introduced during the period 1862-1871, showed significant variation in 13 of 16 skeletal characters for males, while females showed differentiation in only eight characters (Baker 1980). Analysis of variation of 28 morphometric characters in the introduced New Zealand populations of the Common Myna (Acridotheres tristis) revealed that males and females had differentiated in 17 and 13 characters, respectively, within 100 years since their introduction (Baker and Moeed 1979).

Among birds, individuals vary geographically primarily in overall size, which has been correlated with latitude (Johnston and Selander 1973), isophane (Power 1970), latitude and isophane (Baker 1980), temperature (Johnston and Selander 1971; Johnston 1973), and productivity (Niles 1973) suggesting phenotypic adaptation to local environments. The fact that House Finches showed no differentiation in overall size is not consistent with

the thermoregulatory argument of Bergmann. Furthermore, finch morphology in ONT did not support the notion that overall large size is advantageous in seasonal environments because it may confer increased fasting potential during periods of low food availability in winter (Boyce 1978; Murphy 1985). Nevertheless, House Finches in ONT were significantly heavier than in CAL, which may enhance survivorship during periods of food shortage.

Significant interlocality variation in the proportioning of body parts of House Finches suggests adaptive differentiation in accordance with Allen's ecogeographical rule. Birds in ONT showed negative covariation of extremities (limb and skull attributes) with body core parts and weight. This was particularly evident in females. Thus, compared to CAL birds, individuals of the ONT sample had smaller extremities relative to certain core parts and weight. Such proportioning of body parts results in a smaller surface-to-volume ratio, which may be selectively advantageous during cold winter conditions. A small surface-to-volume ratio may permit reduced metabolism and loss of heat (Kendeigh 1969, 1976; Blem 1974); factors of particular importance to birds inhabiting temperate regions where low winter temperature may result in substantial mortality (Fretwell 1972). Similar patterns of character proportioning have been noted for geographical comparisons among populations of House Sparrows (Packard 1967; Johnston and Selander 1971; Johnston 1973), Horned Larks (Eremophila alpestris, Niles 1973), and other species (Mayr 1956).

Geographical patterns of phenotypic variation are believed to be the result of adaptation to local environments. However, the extent to which phenotypic variation reflects underlying genetic variation remains in question. When patterns of morphological variation correlate with environmental gradients it is impossible to differentiate between genetic and environmentally induced variation (Gould and Johnston 1972). Phenotypic responses to environmental factors are common, and thus morphological variation need not imply evolution of characters. James (1983) used transplant experiments to estimate the environmental component of morphological differentiation in Red-winged Blackbirds (Agelaius phoeniceus). Reciprocal transplants of eggs between morphologically distict populations of blackbirds revealed a significant environmental component to interlocality shape variation in nestlings, which reflected morphological differences between adult populations. Further, the extent to which variation in shape was genetically based, varied geographically.

The extent to which morphology in House Finches is environmentally influenced is not known. However, the limited scale of interlocality differentiation found in this study may provide some insight. If morphological differences between the populations were largely the result of environmental factors, why did House Finches in ONT not show differentiation in all or many characters? On the other hand, there is no reason to a priori assume that selective constraints operate at the same level on all characters, let alone equally on similar characters

between localities. For example, interlocality variation of body weight in House Finches may have been the result of geographical differences in feeding conditions. Thus, patterns of character covariation relative to weight may not represent adaptive differentiation. In this regard, however, it is difficult to explain the different patterns of character differentiation shown by the sexes. The degree to which finch morphology is environmentally induced can only be determined through population transplant experiments. Some genetic basis for observed variation may be claimed if patterns of character variation are maintained following reciprocal transplants or explants of phenetically distinct populations.

Alternaltively, natural selection on morphological traits may be inferred if patterns of character covariation are similar among populations existing in climatically different environments (Johnston 1973). Despite a limited scale of interlocality differentiation in introduced New Zealand Commom Mynas, skeletal characters were similarly covariant among populations suggesting an early stage of adaptive differentiation (Baker and Moeed 1979). A similar conclusion was reached by Baker (1980) for introduced populations of House Sparrows in New Zealand, which demonstrated similar patterns of character covariation to North American and ancestral European populations. That female House Finches showed similar patterns of skeletal character covariation on PC II between localities provides some evidence against a solely ecomorphological interpretation of the observed differentiation and suggests that House Finches in ONT

may be demonstrating initial adaptive differentiation. Recently established House Finch populations in British Columbia (Woods 1968) and southeastern United States (Mundinger and Hope 1982; Bystrak 1981) provide an excellent opportunity to assess the integrity and degree of character covariation across North America.

The limited scale of morphological differentiation between localities may be due to the relatively brief period of time eastern House Finches have had to adapt to local conditions. House Finches have been present in eastern North America for only about 44 years, which may represent too little time for natural selection to have an appreciable affect on morphology. Evidence to support this notion is provided by Power (1979) who found that recently established House Finches in Idaho and Washington were phenetically indistinguishable from resident populations in northern Baja, California and San Diego County, California. The fact that House Finches have been present in northwestern United States longer than have birds in eastern North America (Woods 1968) coupled with the similarity in climate between ONT and the Idaho-Washington area (Climatic Atlas of the United States 1968; Climate of North America 1974) is evidence of rapid, albeit limited, morphological differentiation in the introduced population in ONT.

Founder effect

Several studies have noted less variation among introduced than ancestral populations (Johnston and Selander 1971, 1973; Baker and Moeed 1979; Baker 1980) suggesting constraints exist on

differentiation, which may have resulted from restricted variability in founding populations. A founding population (Mayr 1970) represents only a small portion of the genetic variablity present in the parental population, and thus colonizing populations are genetically unique. The eastern House Finch population that now occupies much of the northeastern United States originated from less than 100 birds in total that were released in three localities on Long Island, New York in 1940 (R. S. Arbib, pers. comm.; Elliott and Arbib 1953). Therefore, observed differentiation may be the result of restricted variation in the inoculum samples. Insight may be gained by examining character variances (Johnston and Selander 1971; Power 1971). Consistently smaller character variability in the eastern House Finch population might be indicative of founder effect. However, in this study, virtually all character variances were statistically homogeneous between localities, which suggests that interlocality differentiation is not the result of founder effect.

Sexual dimorphism

House Finches demonstrated a limited amount of differentiation between the sexes. Intersexual variation was found for only four characters in ONT and five in CAL. Males were larger than females for all but one character (FEML in CAL). However, sexual differences appeared to involve shape rather than size as borne out by the discriminant analysis, which indicated that males possessed a relatively larger flying apparatus and

smaller hind limbs than females. The degree of sexual dimorphism did not vary significantly between localities.

Recent literature on the morphometrics of House Finches suggests that males are larger in some characters than females, though the data available are only for external measurements. Across 21 island and mainland sites in California males averaged generally larger bill depth, width and length of wing, tail, and tarsus (Power 1980). Similarly, mean lengths of wing, tail, middle toe, and exposed culmen were generally larger for males in seven ecogeographical regions of the conterminous United States (Aldrich and Weske 1978). However, these differences were not tested statistically. Aldrich (1982) found that significantly longer wings and tails were common to both indigenous (western) and introduced (eastern) males, though males in the west also possessed signififcantly longer culmens and middle toes than females.

There is no evidence in this study that sexual dimorphism may result in differential niche partitioning between the sexes (Selander 1966, 1972; Downhower 1976) since bill dimensions did not vary significantly between the sexes (cf. Aldrich 1982). House Finches probably utilize food resources that occur in sufficient quantities (Beal 1907; Bergtold 1913; Palmer 1972) to allow considerable overlap in diet between the sexes.

Sexual dimorphism in House Finches may be attributed to sexual selection on male morphology. Relative to body weight, which did not vary significantly between the sexes, males showed disproportionately longer and wider wings, longer wing bones, and

shorter leg bones than females suggesting that males are involved in more flying activity. Longer wings may impart a selective advantage to males in defence from other males or control of, a newly secured mate, nest site, or food source, and in the establishment of social hierarchies (Thompson 1960a, 1960b; Selander 1972). However, the limited scale of dimorphism suggests comparable selection intesities on the sexes, which may be due to the semicolonial nesting habits of the species (Thompson 1960b).

Comparison of the degree of sexual dimorphism between ONT and CAL suggested that the proportioning of body elements between the sexes was not locality specific. In the House Sparrow Johnston and Selander (1973) demonstrated a clinal variation in the degree of sexual size dimorphism, which increased with latitiude. Associated with this clinal variation in dimorphism is selection for optimal size (Bumpus 1899; Grant 1972; Johnston et al. 1972; Rising 1972; Johnston and Fleischer 1981; Fleischer and Johnston 1984) and shape (Fleischer and Johnston 1982) at the intralocality level, which is most intense in winter. Despite considerable variation in environmental conditions among the Galapagos Islands (Abbott et al. 1977), Price (1984) found no significant difference in the degree of sexual dimorphism among populations of Darwin's finches. Size distributions of both sexes of Darwin's Medium Ground Finch (Geospiza fortis) responded similarly to the effects of drought-mediated selection. Large birds that possessed large bills survived best because they could crack the large and hard

seeds that predominated in the drought (Boag and Grant 1981).

Differentiation of morphological characters of introduced House Finches has not resulted in an increase in sexual dimorphism suggesting that selection on the dimorphism does not vary geographically. However, the fact that the sexes showed interlocality differentiation with respect to different characters, yet the degree of dimorphism remained geographically invariant, is confusing. The presence of statistical 'noise' (unwanted variation) may generate spurious patterns of character covariation, particularly if multivariate vectors of variation are simple in structure (i.e. only a few characters contributing to discriminate between samples). However, samples were multivariately normal and the sexes were distingished primarily on the same characters in separate DFAs for each locality. On the other hand, multivariate measures of distance between sample centroids have the disadvantage of being completely blind to patterns of character covariation that contribute to the discrimination of samples. Thus, different sets of characters and the counterbalancing effects of their associations may generate a similar degree of sexual dimorphism between localities. This appears to be occurring in House Finches. In such instances more insight may be gained by examining the character variation univariately. In House Finches, however, it is difficult to assign a functional explanation for the locality differences given the small scale of differentiation shown between the sexes in ONT and CAL.

The nesting season

Egg dates of House Finches from southwestern California usually range from late February to early August (Woods 1968). The most intensive nesting occurs during April and May (Bergtold 1913) with some continuing through June and into July (Woods 1968). The earliest reported nesting was in Colorado on 30 January (Woods 1968) and the latest on 24 November in California (Smith 1930).

Of 64 museum clutches examined from Los Angeles County, the frequency of collection per month was: 3.1% in March, 43.8% in April, 37.5% in May and 15.6% in June. Although oological collections generally show bias in collection time (Lack 1946), House Finches are very common in southwestern California and the frequency of clutch collection date probably reflects breeding intensity. Thus, data that were collected in CAL during the period 2 March - 20 May represent the bulk of the breeding season.

In ONT the mean egg laying date showed no significant annual variation; the onset of breeding differed by only three days between years. Egg-laying in CAL started approximately three months earlier than in ONT.

Holcomb (1969) suggested that laying date in American Goldfinches (Carduelis tristis) is mediated by temperature and precipitation; the limited seasonal data for ONT support such a relationship. The lack of temporal data for CAL prohibits the correlation of such proximate cues to the timing of breeding, however, it is unlikely that the onset of breeding in CAL is

determined by temperature as the breeding season is less thermally restrictive than in ONT. The reproductive cycle of House Finches is probably regulated by photoperiod as is the case with finches in general (Newton 1972). Proximate factors such as temperature and precipitation may be more indicative of future food availability. Middleton (1979) noted that many weedy plant species show very little annual variation in their time of flowering, and thus may serve as indicators of future seed crops for granivorous birds. House Finches forage on dandelions (Taraxacum officinale, pers. obs.) and may feed their young almost exclusively on the seeds of this weed (Bergtold 1913). Thus, the spring emergence of dandelion flowers as well as the flowers of other weeds may serve as the ultimate factor in mediating the time of nesting in House Finches.

In 1984, CAL experienced a very dry breeding season. Such conditions may delay breeding (Murphy 1983), while periods of high temperature and/or low precipitation may curtail egg-laying (Murphy 1978a). Presumably such conditions result in food shortages, which deprive females of sufficient nutrients for egg formation. House Finch males provide females with feedings but do so usually during incubation (Woods 1968) and not before or during nest construction (Anderson and Anderson 1944). Thus, the feeding of females by males cannot play a nutritional role in egg formation (Wiggins 1984), which might allow females to lay eggs during environmentally stressful periods. Because of their primarily granivorous diet (Beal 1907) House Finches are probably less affected by prevailing weather conditions than insectivorous

species and may be able to breed successfully during periods of low precipitation and/or high temperature.

Clutch size

Clutch size did not differ significantly between localities, nor between years in ONT. A significant decrease in clutch size during the course of the breeding season is evident only for ONT in both years.

House Finches usually lay four or five eggs, though clutch size may range from two to seven eggs (Wagner 1957; Woods 1968). Gill and Lanyon (1965) reported that at Huntington, New York, the clutch size of eight nests ranged from four to six and averaged 4.75 eggs, comparable to clutch size means found in this study. Wagner (1957) examined 20 nests in Mexico City, Mexico and found that 17 contained only two eggs and three contained three eggs. Thus, geographical variation in the clutch size of the House Finch is in accordance with the trend of increased clutch size at higher latitudes (Lack 1954).

Although a difference in clutch size between localities was not found in this study, introductions of other species to geographically new environments at different latitudes has resulted in a change in clutch size. A decrease in clutch size has been noted for the European Goldfinch (Carduelis carduelis, Frith 1957) and the Ring-necked Pheasant, (Phasianus colchicus, Westerskov 1956) following introductions from England to Austrailia and New Zealand, respectively. However, the factors responsible for such changes are not known.

The similarity in clutch size between ONT and CAL may be a result of the small difference in latitude between study sites, which was approximately 8° 51' (cf. Svensson 1978; Murphy 1983; Møller 1984). Although day-length increases with latitude during summer, a restricted range in latitude would represent little variation in day-length. Thus, birds in ONT would not have substantially more time to feed nestlings than in CAL and, as a result, might not be able to raise larger broods (Lack 1954). Royama (1969) related brood size to food availability, time available for parental foraging and ambient temperature. Since temperature decreases with increase in latitude, he suggested that at higher latitudes the greater thermal inertia of larger broods would decrease the energy requirements of individual nestlings and permit the rearing of more young. Although aspects of food availability were not determined in this study (but see below), ambient temperature during the breeding season was similar between localities. Thus, it is unlikely that the energy requirements of nestlings differed greatly between study sites. Furthermore, the variation in population age structure between localities is unknown. However, the exponential increase of House Finch numbers in the east (Bock and Lepthien 1976; Mundinger and Hope 1982) and seasonal decline of clutch size (Perrins 1965; 1970) observed in ONT suggests a skewed age distribution. A greater proportion of first time breeders in ONT than in CAL may depress clutch size (Perrins 1965; Middleton 1979; Haymes and Blokpoel 1980) and mask geographical differences.

Coinstantaneous measurement of the many proximate factors that determine clutch size is impractical and some have focused only on the seasonality of available food resources in an attempt to explain geographical trends in clutch size. Ricklefs (1980) and Koenig (1984) used actual evapotranspiration as a measure of primary productivity to test Ashmole's (1963) hypothesis that clutch size is related to available food resources relative to the density of the breeding population. They found that geographical differences in clutch size correlated strongly with patterns of resource fluctuation during the season, as predicted by Ashmole. Northern latitudes experience relatively low productivity during the winter, which may result in substantial mortality. The relatively small number of survivors benefit the following breeding season from abundant food resources. Thus, compared to southern populations, northern populations are assumed to show greater fluctuation in numbers. In the eastern United States the size of wintering populations of House Finches is increasing rapidly (Bock and Lepthien 1976; Mundinger and Hope 1982) indicating that the rate of recruitment is greatly exceeding the rate of mortality. Assuming that the winter months in ONT represent a period of low productivity, House Finches apparently are not experiencing limited food resources during the nonbreeding season. Possible explanations for decreased winter mortality may include the extensive use of feeders (Elliott and Arbib 1953; Dunn 1984), the adoption of a migratory habit in the east (Cant and Geis 1961) and superiority over potential competitors (Kricher 1983). Such factors would result in

seasonally more stable populations, and thus obscure the inverse relationship between clutch size and winter productivity (Ricklefs 1980; Koenig 1984). Based on North American Nest Record Card Program data, Wootton (1986) compared clutch size of parental (southern California) and introduced (states east of Indiana and north of North Carolina) populations of House Finches and found that eastern birds produced significantly larger clutches than their western counterparts. He suggested a smaller House Finch population density in the east to account for the observed difference, but never considered geographical variation of clutch size or the time frame in which data were collected in the east, which may have resulted in a significant difference of clutch size between parental and introduced populations. Geographical variation of clutch size of the House Finch merits further study.

Clutch size and egg weight: seasonal variation

Clutch size was negatively correlated with time of laying in ONT but showed no significant seasonal trend in CAL. Variation in mean egg weight was not dependent on the date of clutch initiation in ONT but showed a highly significant seasonal increase in CAL.

Seasonal decline in clutch size, which is demonstrated by many species, is thought to be an adaptation to decreasing food resources (Lack 1966; Perrins 1970). Food availability at the time of laying is not believed to determine clutch size, but rather that clutch size is adapted to the poor food resources

available for nestlings late in the season. Natural selection will favour those individuals that are able to guage clutch size according to future food resources. Thus trends in clutch size would represent 'true' adjustments or adaptations to maximize fledging success. However, such adjustments in reproductive output are only possible in stable environments where individuals can predict future food supplies. In environments where food supply may fluctuate unpredictably or when food supply is more abundant later in the season, declines in clutch size with advance of the breeding season are not adequately explained by deterioration of the food availability.

By far the largest proportion of the total diet of House Finches is composed of seeds from weedy plants (Beal 1907). The overlapping and long flowering periods (45-55 days) of many ephemeral plant species (Heinrich 1976) may provide ample if not increased food resources later in the season. Urban and cultivated areas provide additional food in the form of table refuse (Bergtold 1913) and fruit crops (Palmer 1972). Thus, it seems unlikely that finches would be food-stressed late in the breeding season.

The compromise between maximum reproductive output and quality of young may show seasonal trends in terms of the number of eggs laid and the size of eggs (see Williams 1966). If environmental conditions deteriorate with advance of the breeding season, greater fledging success may be realized with fewer but better provisioned eggs and nestlings (Perrins 1965; Murphy 1978b; Schifferli 1973). Alternatively, large clutches may be

produced early in the season at the expense of egg size since conditions for raising young are probably more favorable (Lack 1966). In ONT seasonal trends in clutch size and egg weight do not appear to demonstrate adaptive shifts in resource allocation, since small clutches late in the season did not contain relatively heavy eggs. Similarly, in CAL the seasonal increase in egg weight was not associated with a decline in clutch size. In the Great Tit (Parus major) seasonal decrease in clutch size was associated with a corresponding increase in egg weight (Perrins 1970). Perrins (loc. cit.) attributed the increase in egg weight to an increase in food supply and argued that late nesters initiate their clutches when most early nesters are feeding their young, presumably during the seasonal peak in food availability. He further suggested that small late clutches, therefore, cannot be attributed to impoverished food conditions at the time of laying and must represent an adaptation for maximizing the number of surviving offspring. Observed trends in egg weight between localities suggest that food supply was relatively constant throughout the breeding season in ONT but increased in CAL. If decline in clutch size represents an adaptive adjustment to food availability, seasonal patterns of clutch size and fledging success should coincide. The fact that large clutches early in the season produced equally as many young as did small late clutches indicates that reproductive success is not dependent on the time of laying in ONT (Spearman rank coefficient of correlation, $r_s = -0.02$, $N = 14$, $P >> 0.05$ (ONT 1983); $r_s = 0.16$, $N = 5$, $P >> 0.05$ (ONT 1984)). Similarly in CAL

fledging success showed no significant seasonal trend as predicted (r_s = -0.23, N = 20, P >> 0.05). Consequently, the observed seasonal decrease of clutch size in ONT does not appear to demonstrate an adjustment to decreasing food availablity, but rather may represent physiological or behavioral constraints on late nesting individuals.

In several species females breeding for the first time produce smaller clutches and are less successful in rearing young than older individuals (Perrins 1970; Middleton 1979). Furthermore, young individuals tend to start laying later in the season than older birds (Klomp 1970; Perrins 1970), which may contribute to a seasonal decline in clutch size. In the American Goldfinch the percentage of clutches laid by old birds (> 1 year) decreased with advance of the season, the largest proportion of late nests were initiated by females of unknown age, probably mainly 1st-year birds (Middleton 1979). Presumably, such variation in laying date is the result of differences in foraging ability among females; young individuals are less experienced at foraging, and thus require a longer period of time to aquire sufficient nutrients to commence egg laying than older individuals. Alternatively, the slower rate of gonadal development in younger individuals may prevent them from breeding early in the season (Murton et al. 1974; Middleton 1978). The increasing population size of House Finches in the east indicates that the proportion of young individuals in the breeding population is high. This interpretation is supported further by the fact that fledging success was significantly

greater in CAL than in ONT (Kruskal-Wallis one-way ANOVA: $X = 9.202$, $P = 0.01$, mean ranks and (N): 23.8 (19), 12.0 (6), 30.8 (20) for ONT 1983, ONT 1984 and CAL 1984, respectively) with birds from CAL fledging an average of 4.12 chicks per pair compared to ONT means of 3.53 (1983) and 2.50 (1984) chicks per pair. Therefore, in ONT the seasonal decrease in clutch size may have been the result of young individuals breeding later in the season. If so, the observed trend should disappear once the population reaches the carrying capacity of the environment and assumes a stable age distribution. Future surveys of House Finches breeding in ONT may reveal a lack of seasonal variation in clutch size similar to that observed in CAL.

Egg size

Interlocality variation

Females on average laid significantly larger (+8.9% in volume) and heavier (+9.4% in weight) eggs in ONT than in CAL. The lack of annual variation of egg size in ONT and in CAL (from the L. A. Co. museum sample) suggests that interlocality differences are not the result of sampling effects, but instead represent differentiation in egg size. Geographical differences in egg size have also been observed in House Sparrows (Murphy 1978a) and Eastern Kingbirds (Murphy 1983).

Among 13 species of Emberizids, 98% of the variation in mean egg weight was explained by differences in mean body weight (Rahn et al. 1975). Järvinen and Väisänen (1983, 1984) found that that heavy Pied Flycatcher (Ficedula hypoleuca) females produced larger and heavier eggs than light females. King and Hubbard (1981) used wing length as a measure of body size in White-crowned Sparrows (Zonotrichia leucophris) and found that geographic variation in mean egg weight was largely explained by geographic differences in wing length. Similarly, mean egg weight showed a significant positive correlation with female wing length in the Fieldfare (Turdus pilaris, Otto 1979). Therefore, interlocality differences of mean egg weight and size in the House Finch may be expected to vary according to geographical differences in female weight as supported by my data. Female House Finches were significantly heavier in ONT than in CAL, and thus laid correspondingly heavier and larger eggs. The weight of European Starling eggs is determined by

their albumen content (Ricklefs 1977), which has been related to the weight of the oviduct (Ricklefs 1976). Thus, larger House Finches in ONT probably possess the physical means for producing larger eggs.

Murphy (1983) found no correlation between geographical differences in mean egg weight and body size of adult Eastern Kingbirds and mentioned the possibility of thermal adaptation as an explanation for the larger size of eggs in New York State. In ONT mean monthly ambient temperature during the breeding season is greater than in CAL, therefore, the occurrence of larger eggs in ONT does not support a thermoregulatory argument for geographical differences in egg size in the House Finch. Proximate factors of temperature (Ojanen 1983a) and precipitation (Murphy 1983) appear to have little influence on egg size in the Great Tit, Pied Flycatcher and Eastern Kingbird, respectively. Similarly in House Finches, egg size is apparently not sensitive to the proximate effects of weather, since for Californian samples egg size was not found to differ significantly between museum samples and those collected during the unusually hot and dry conditions in CAL in 1984.

Seasonal variation of egg weight in CAL suggests that egg weight is related to food availability as suggested elsewhere (Perrins 1970; Murphy 1978b), which may result in geographical differences. Otto (1979) found that mean egg weight per clutch in Fieldfares was dependent on the density of breeding individuals within colonies; smaller eggs were present in colonies with a higher number of breeding individuals. Since egg

size was also correlated postively to the biomass of lumbricids (the primary food), Otto suggested that egg size was mediated by the amount of food available per nest. Since House Finches are localized feeders (Palmer 1972) the potential exists for a depletion of food resources near nesting areas. Although a quantitative assessment of the breeding densities of House Finches was not carried out, the breeding density in CAL was appreciably greater, however, birds did not appear to be food stressed. European Starlings (Karlsson 1983 in Slagsvold et al. 1984) responded to supplementary feeding by laying larger eggs. Conversely, larger eggs were laid during periods of poor food availabiltiy in Wood Pigeons (Columba palumba, Murton et al. 1974) and Red-billed Gulls (Larus novaehollandiae, Mills 1979), and thus the relationship between food supply and egg size varies markedly among species.

Moss and Watson (1982) eliminated effects of the environment on the reproductive output of Red Grouse (Lagopus lagopus) by rearing captive individuals and measuring egg size in subsequent generations. They found that egg size had a large heritable component (0.7 ± 0.2) and that much of the variation was due to female individuality. High heritabilites for egg volume exist in Great Tits (0.86 ± 0.29, Ojanen et al. 1979; 0.61 ± 0.25, Van Noordwijk et al. 1980) and the large phenotypic effect of female individuality (60-80%) on egg size has been interpreted as a rough measure of additive genetic factors (Ojanen et al. 1979; Van Noordwijk et al. 1981). Because measurements of breeding individuals were not taken in this study, estimates of

the heritability of egg size could not be made. However, the large interclutch variance components for egg weight (78-80%) found in this study suggest a large genetic component to egg size in the House Finch. Demonstration of a high heritability of egg size in the House Finch would imply that egg size is sensitive to differential selective pressures, which could rapidly change the average size of eggs between populations provided that the effects of selection are constant and occur in the absence of gene flow (e.g. Festing and Nordskog 1967).

The House Finch population in ONT occurs in a markedly different environment from that of the CAL population. The breeding season in ONT is shorter and winter mortality is probably greater than in CAL. Thus, selective pressures operating to increase winter survival probably affect the reproductive output of ONT individuals. Large eggs contain more nutrients (Ricklefs 1977; Ojanen 1983b), which may give individuals the advantage of increased growth rate (Schifferli 1973) and subsequent increased chances of survival (Parsons 1970; Nisbet 1973).

Intraclutch variation

The differential provisioning of eggs within a clutch is widespread in birds and is believed to have an ultimate adaptive value (Howe 1976; Slagsvold et al. 1984). In this study a trend of increasing egg weight with sequence of laying is evident in clutches of four but egg weight did not vary in equally common clutches of five. Howe (1976: 1204) suggested that

"higher provisioning in the last egg enhances the competitive position of the chick most disadvantaged by hatching sequence", since eggs usually hatched in the order in which they were laid. The fact that House Finch clutches hatch asynchonously and tend to hatch in the order in which they are laid (pers. obs.), suggests that the disadvantage of hatching later in four egg clutches may be lessened if young hatch from larger, well provisioned eggs. Such a modification of egg size is apparently most adaptive in environments where food conditions vary unpredictably (Howe 1976), and therefore broods are kept alive as long as possible but younger individuals starve if food becomes scarce. Thus, differences of egg weight within a clutch as a mechanism for increasing survival of young would seem most appropriate in larger clutches and this seems to be the case for some species (Howe 1976, 1978; Zach 1982).

For granivorous species food supply probably does not vary independently of time, which may explain the lack of egg size variation in clutches of five. Furthermore, of successful nests in CAL, clutches of five fledged significantly more chicks per breeding pair ($\bar{x}$ = 4.58, SD = 0.67, N = 12 clutches) than clutches of four ($\bar{x}$ = 3.75, SD = 0.71, N = 8 clutches; Mann Whitney U = 17.5, $P < 0.01$, N = 8,12), suggesting that in clutches of five, late-hatching young are not at a disadvantage since increase of egg weight with laying sequence in clutches of four did not ensure the fledging of all young within a brood.

Different patterns of resource allocation to eggs within a clutch may reflect differences in the age of parents and their

foraging abilities. Although the age of breeding females was not known in this study, in some species younger females generally lay smaller clutches (Perrins 1970) and are less efficient at parental foraging (Perrins 1970; Mills 1979). Nestlings that hatch later in four egg clutches may experience a disadvantage in terms of poor feeding rates from a young female or parents. Hatching from a larger egg may act to offset this disadvantage. However, such an explanation is at best speculative and more data are required concerning the relationship between egg size, nestling survival, and demographic and environmental factors.

Nestling size and growth

Compared to CAL, ONT nestlings were significantly heavier on day of hatching and apparently grew at a faster rate than those in CAL. ONT nestlings were generally larger throughout the growth period and on day 13 were significantly larger in terms of weight, bill depth and manus length, which suggests that fledglings in ONT were larger than in CAL.

In many avian species, a positive relationship has been found between fresh egg weight and the weights of newly hatched young (e.g. Schifferli 1973; Murphy 1983; Richter 1984; Rofstad and Sandvik 1985). Similarly, in House Finches large eggs produced nestlings of significantly greater weight at hatching than small eggs, in both localities. Nestlings may benefit from a greater weight in several ways. In the Herring Gull (Larus argentatus), Parsons (1970) found a significant relationship between egg volume and lipid content of newly hatched chicks. A larger nutrient reserve in House Finch hatchlings could increase the chance of survival during early nestling life. Assuming that ONT is a more variable environment during the breeding season, temporary food shortages are probably more frequent in ONT than in CAL. The ability of nestlings to fast for short periods of time may be advantageous in a relatively unpredictable environment such as ONT. Alternatively, hatchlings may be larger in overall body size. In addition to weight, ONT hatchlings are larger in terms of bill length, bill depth and tarsometatarsus length than CAL individuals suggesting that ONT young hatched at a more advanced stage of development. Larger young at hatching

have a head start in growth, which may result in earlier fledging (Gibb 1950; Perrins 1970; Järvinen and Ylimaunu 1986).

Size at hatching may also affect rate of growth. Schifferli (1973) demonstrated that heavier Great Tit chicks at hatching grew more quickly than lighter ones. In this study, the variation in magnitude of F-ratios among samples for weight at hatching and 13 days suggests that increase in weight was faster for ONT individuals. Since the breeding season in ONT is shorter than in CAL, young have a limited amount of time for additional growth post fledging. Thus, nestlings in ONT may be under strong selection pressure for rapid growth and development before fledging. Evidence for an increase in growth rate in a shorter breeding season is provided by only one other species. Maher (1980) found that arctic races of the Horned Lark grew faster than nestlings of temperate races. However, growth rates in other species appear to be geographically invariant (e.g. White-crowned Sparrows, King and Hubbard 1981; Eastern Kingbirds, Murphy 1983).

Nestling weight at fledging is believed to be an important factor in determining the survival of fledlings. Perrins (1965) demonstrated that heavier Great Tit fledglings survived better during the immediate post fledging period than lighter fledglings. He suggested that such differential survival could be due to differences in fat deposits of fledglings. Garnett (1981) proposed that body size has a more direct effect on survival in that body size may dictate the number of aggessive encounters a fledgling dominates. Although post fledging

survival of House Finch young was not assessed, the rapid increase in size of the eastern population is indicative of substantial fledgling survival. Data on variation in weight, bill depth and manus length of individuals from the two populations suggests that nestlings in ONT fledge in a more advanced stage of growth than in CAL.

Temporal and geographical variation in nestling weight at various stages of the growth period may be considerable (Ricklefs 1968; O'Connor 1977; Ricklefs and Peters 1979; Ross 1980) and influenced by several environmental factors, especially food availability (van Balen 1973; Bryant 1978; Quinney et al. 1986). Except for manus length, ONT nestlings showed no variation in size (at 13 days of age) between years, which suggests that the effects of proximate factors on growth were similar between years. However, CAL nestlings experienced a very hot and dry season in 1984 that may have been responsible for exaggerated differences in nestling size between the two localities. Evidence against the idea of environmentally influenced nestling growth in CAL can be provided by a positive correlation of nestling weight with egg weight and adult weight. Schifferli (1973) found that the body weight of nestling Great Tits was influenced by their egg weight until the young were 14 days old. In domestic fowl, egg weight has a significant effect on the chicks' body weight for as long as 9 (Wiley 1950) to 12 (Skoglund et al. 1952) weeks. In CAL, nestling weight on day 13 showed a significant and positive relationship with fresh egg weight (r_S = 0.74, N = 8, P < 0.05), which suggests that egg

weight in House Finches influences the growth of nestlings.

Between locality differences in the lengths of bill and tarsometatarsus disappeared on day nine, and on day 13 for wing length (in 1984). Interlocality differences in the growth of these characters were manifest in the adjustment of the pattern of growth between hatching and 14 days of age. Such variation indicates tradeoffs in growth in which the allocation of resources for growth in these characters was disproportionately greater in CAL nestlings. That growth in bill, wing and tarsometatarsus length of CAL nestlings was independent of changes in weight, bill depth and manus length suggests that real differences in nestling growth between localites may be present (cf. Murphy 1983).

SUMMARY AND CONCLUSIONS

House Finches in Ontario showed significant differentiation in morphology and reproductive traits from those in California. Although interlocality differentiation in skeletal and external characters was limited in scale, multivariate analysis of character variation based on total correlation matrices revealed meaningful patterns of character covariation. Appendicular bones and certain skull attributes were negatively covariant with certain body core parts and particularly weight (especially in females) suggesting that variation in shape reflected a set of thermoregulatory size adaptations as proposed by the ecogeographical rule of Allen (Mayr 1970). However, important to the interpretation of such differentiation concern its degree and the extent to which morphological variation may be attributed to evolution and how much is really environmentally induced (e.g. James 1983). In my study, both sexes showed significant shape differentiation between localities. Because the sexes also showed interlocality differentiation with respect to different characters, and because females showed similar patterns of character covariation on PC II between localities, I suggest that finches in ONT may be demonstrating initial adaptive differentiation in response to local environmental conditions.

Morphological differences are also a function of size and shape entrainment to aspects of behaviour and physiology, which were not assessed in the present study. House Finches from southern California are known to acclimatize readily to colder climates (Dawson *et al*. 1983) and this physiological

flexibility in concert with behavioural changes in ONT may have minimized differences in morphology between the two populations. This may explain why House Finches in ONT showed such a limited scale of differentiation and no geographical variation in overall size. Further, replicate sampling or jacknifing of samples (Gibson et al. 1984) should be done in order to determine the stability of character relationships. The notion that finches in ONT have differentiated adaptively to a novel environment may be strengthened if future sampling in ONT reveals an increase in the degree of character differentiation and covariation.

House Finches in ONT also demonstrated differentiation in certain reproductive traits. Although there was no difference in clutch size between localities, females in ONT laid significantly larger eggs, which gave rise to significantly larger nestlings than in CAL. Further, nestlings in ONT appear to have increased in weight faster than nestlings in CAL. Several results suggested that egg size and nestling size differences between localities may not have been solely the result of intralocality variation. First, eggs in ONT were laid by significantly heavier females than in CAL. Thus, egg size appears to be related to female body weight in House Finches. Second, egg size did not show any annual variation in ONT and CAL (from the L. A. Co. museum sample) suggesting that interlocality differences in egg size are not the result of sampling effects but may represent real differences in egg size. Finally, in CAL a significant correlation between fresh egg weight and nestling weight at 13 days suggested that egg weight influenced the post natal

development of House Finch young.

Finches in ONT experience a shorter breeding season and more severe winters than those in CAL, and thus selection may favour larger eggs and young. Larger eggs may contain a larger nutrient reserve, which may result in heavier nestlings at hatching, faster growth of young, and fledging of young at a heavier weight. Heavier young at fledging may increase the chance of survival during the immediate post fledging period and may offset the pressure for additional growth post fledging. This is particularly relevant in ONT were fledglings have a relatively short period of time for additional development prior to the onset of winter.

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Appendix 1. Suitability of the study areas.

Although the introduced eastern population of House Finches was not sampled at its 'centre' (i.e. Long Island, New York) but rather at its periphery in ONT, the choice of the ONT study area is appropriate for the assessment of morphological and reproductive differentiation of eastern birds, which have colonized a novel environment. Populations may differ geographically because of selection pressure on individuals or stochastic processes, which include founder effect and random-genetic-drift[1]. House Finches in eastern North America have rapidly expanded their range, hence in newly occupied areas (i.e. the periphery of the expanding population) individuals may experience a reduction in variability due to partial founder effect[2]. Alternatively, gene flow from the centre to the margin of a population may be small since, in general, individuals disperse only small distances relative to their geographical range[3], which may result in differentiation of marginal populations via isolation-by-distance. Thus, any differentiation of ONT House Finches may be explained equally as well by the action of natural selection on individuals or by a random-genetic-drift (isolation-by-distance) model. However, an extremely small amount of gene flow is necessary to decrease the rate at which a population differentiates from other populations[4]. House Finches are capable of long-distance (jump-) dispersal[5], and thus the long-distance dispersal of only a small number of House Finches may be sufficient to maintain genetic variability in marginal populations such as ONT.

Furthermore, the rapid increase of House Finch numbers in the east suggests that any variability lost through random-genetic-drift may be reconstituted by mutation and recombination[6].

1
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Mundinger, P.C., and S. Hope. 1982. Expansion of the winter range of the House Finch: 1947-1979. Amer. Birds 36:347-353.

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Appendix 2. Listing of agencies, volumes and years of Climatological Data for the United States to January 1983.

Weather Bureau. Climatological data. California. - v. 69, no. 12 (Dec. 1965).

Environmental Science Services Administration. Climatological data. California. v. 70, no. 1 (Jan. 1966) - v. 74, no. 8 (Aug. 1970).

Environmental Data Service. Climatological data. California. v. 74, no. 9 (Sept. 1970) - v. 82, no. 5 (May 1978).

Environmental Data and Information Service. Climatological data. California. v. 82, no. 6 (June 1978) - v. 86, no. 12 (Dec. 1982).

National Environmental Satellite Data and Information Service. Climatological data. California. v. 87, no.1 (Jan. 1983).

Appendix 3. Standard avian fat codes used by the Royal Ontario Museum, Toronto, Ontario.

No Fat - Nil

None at all or hardly a trace in the dorsal tract or around the pygostyle and furcula.

Light Fat - Lt.

A thin depth, perhaps 0 to 0.5 mm in depth in the ventral tracts. Some fat in the furcula.

Moderate Fat - Med.

Moderate in tract areas, with small plates elsewhere on the skin. Substantial fat in the furcula. Perhaps 0.5 to 1.0 mm in depth.

Heavy Fat - Hea.

Moderate sheets, removable as such from many parts of the skin. Perhaps 1.0 to 1.5 mm in depth. Furcula filled.

Extremely Heavy Fat - Ex. Hea.

Considerable amounts of solid fat inside the abdominal cavity. Furcula filled. Sheets of fat removable from skin, 1.5 to 2.0 mm in depth.

Appendix 4. Description of morphological characters.

Skeletal characters:

Skull Length (SKUL) - Medially, from the posterior region of the cerebellar prominence to the tip of the premaxilla.

Skull Width (SKUW) - Transversely, the maximum dimension between the temporal ridges.

Skull Depth (SKUD) - Medially, from the ventral region of the basisphenoid to the dorsal region of the frontal.

Premaxilla Length (PREL) - Lateromedially, from the anterior margin of the narial opening to the tip of the premaxilla.

Premaxilla Width (PREW) - Transversely, the maximum dimension between the posterior tips of the maxilla.

Premaxilla Depth (PRED) - Medially, from the dorsal region of the nasal bone to the ventral region of the jugals, posterior to the tips of the maxilla.

Mandible Length (MANL) - Lateromedially, from the tip of the postarticular process to the dentary symphysis.

Mandible Symphysis Length (MASL) - Medially, from the posterior to the anterior region of the dentary symphysis.

Mandible Depth (MAND) - Medially, from the ventral to the dorsal region of the dentaries at the posterior margin of the dentary symphysis.

Coracoid Length (CORL) - The minimum dimension from the sternal facet to the tip of the acrocoracoideus.

Sternum Length (STEL) - Medially, from the posterior margin of the sternum to the manubrium.

Keel Depth (KEED) - Medially, from the manubrium to the ventral margin of the keel.

Humerus Length (HUML) - The minimum dimension between the intercondylar sulcus and the tip of the head.

Ulna Length (ULNL) - The minimum dimension between the intercondylar sulcus and the tip of the olecranon.

Pelvis Length (PELL) - Lateromedially, from the anterior to the posterior margin of the ilium.

Pelvis Width (PELW) - Transversely, the minimum dorsal dimension between the acetabula.

Femur Length (FEML) - The minimum dimension between the intercondylar sulcus and the tip of the trochanter.

Tibiotarsus Length (TIBL) - The minimum dimension between the retrocristal fossa and the intercondylar sulcus .

Tarsometatarsus Length (TARL) - From the tip of the intercondylar prominence to trochlea for digit III.

External characters:

Tip of Bill to Nostril Length (BNL) - Lateromedially, from the anterior margin of the nostril to the tip of the bill.

Bill Length (BIL) - From the base of the upper rhamphothecus at the feather margin to the tip of the bill.

Bill Depth (BID) - Medially, from the ventral region of the lower rhamphothecus to the dorsal region of the upper rhamphothecus at the base of the bill.

Bill Width, Upper Rhamphothecus (BWU) - Transversely, the maximum dimension at the base of the exposed bill.

Bill Width, Lower Rhamphothecus (BWL) - Transversely, the maximum dimension at the base of the exposed bill.

Wing Length to the Longest Primary (WLP) - The dimension on the closed, unflattened wing from the anterior margin of the wrist joint to the tip of the longest primary.

Wing Length to the Longest Secondary (WLS) - The dimension on the closed, unflattened wing from the anterior margin of the wrist joint to the tip of the longest secondary.

Tail Length (TLL) - From the point where the two middle rectices emerge from the skin to the tip of the longest rectrix.

Tarsometatarsus Length (TSL) - From the tibiotarsal-tarsometatarsal notch to the prominent fold of skin formed by the hallux.

Weight:

Fresh Weight (WEI) - Taken within two hours after collection.

Cube Root of Weight (CWEI).

Appendix 5. Repeatabilites of skeletal character measurements for 15 specimens (N = 3 for each character).

Character	Repeatability
SKUL	1.00
SKUW	1.00
SKUD	1.00
PREL	0.99
PREW	1.00
PRED	0.99
MANL	1.00
MASL	0.99
MAND	1.00
CORL	1.00
STEL	1.00
KEED	1.00
HUML	1.00
ULNL	1.00
PELL	1.00
PELW	1.00
FEML	1.00
TIBL	1.00
TARL	1.00

Appendix 6. Total correlation matrices for males and females used in principal components analyses.

Pearson product-moment correlation coefficient matrix of skeletal characters and weight for male House Finches.

	SKUL	SKUW	PREL	PREW	MAND	CORL	STEL	KEED	HUML	ULNL
SKUL	1.00000	0.18266	0.64799	0.18077	0.50816	0.33991	0.38445	0.32121	0.39464	0.39348
SKUW	0.18266	1.00000	-0.01851	0.09986	-0.02591	0.07442	0.14364	0.16320	0.01281	0.21666
PREL	0.64799	-0.01851	1.00000	0.06713	0.52163	-0.00387	0.19964	0.11022	0.17447	0.13740
PREW	0.18077	0.09986	0.06713	1.00000	0.43206	-0.02728	0.16043	0.12184	-0.01683	-0.14275
MAND	0.50816	-0.02591	0.52163	0.43206	1.00000	0.09457	0.34423	0.29787	0.22555	0.14367
CORL	0.33991	0.07442	-0.00387	-0.02728	0.09457	1.00000	0.44083	0.52367	0.72937	0.74407
STEL	0.38445	0.14364	0.19964	0.16043	0.34423	0.44083	1.00000	0.70435	0.31966	0.24078
KEED	0.32121	0.16320	0.11022	0.12184	0.29787	0.52367	0.70435	1.00000	0.36799	0.36788
HUML	0.39464	0.01281	0.17447	-0.01683	0.22555	0.72937	0.31966	0.36799	1.00000	0.86393
ULNL	0.39348	0.21666	0.13740	-0.14275	0.14367	0.74407	0.24078	0.36788	0.86393	1.00000
PELL	0.48073	0.00079	0.35225	0.01684	0.35172	0.17991	0.24945	0.26826	0.29266	0.30022
PELW	0.09625	0.12370	0.03818	0.05211	0.03934	0.39340	0.14603	0.36688	0.36522	0.34929
FEML	0.39657	-0.04321	0.14047	0.00406	0.33366	0.46283	0.11676	0.22211	0.71626	0.68299
TIBL	0.40787	0.13096	0.12091	-0.05901	0.26450	0.68947	0.29518	0.45502	0.76354	0.85446
TARL	0.41692	0.14848	0.13192	-0.15222	0.12959	0.53999	0.21208	0.25051	0.60020	0.65581
CWEI	0.09954	0.27632	-0.05660	0.29484	0.14950	0.38390	0.42462	0.41425	0.20170	0.16975

	PELL	PELW	FEML	TIBL	TARL	CWEI
SKUL	0.48073	0.09625	0.39657	0.40787	0.41692	0.09954
SKUW	0.00079	0.12370	-0.04321	0.13096	0.14848	0.27632
PREL	0.35225	0.03818	0.14047	0.12091	0.13192	-0.05660
PREW	0.01684	0.05211	0.00406	-0.05901	-0.15222	0.29484
MAND	0.35172	0.03934	0.33366	0.26450	0.12959	0.14950
CORL	0.17991	0.39340	0.46283	0.68947	0.53999	0.38390
STEL	0.24945	0.14603	0.11676	0.29518	0.21208	0.42462
KEED	0.26826	0.36688	0.22211	0.45502	0.25051	0.41425
HUML	0.29266	0.36522	0.71626	0.76354	0.60020	0.20170
ULNL	0.30022	0.34929	0.68299	0.85446	0.65581	0.16975
PELL	1.00000	0.18636	0.45329	0.28301	0.36553	-0.03313
PELW	0.18636	1.00000	0.25621	0.33031	0.36571	0.22578
FEML	0.45329	0.25621	1.00000	0.70679	0.67075	-0.06181
TIBL	0.28301	0.33031	0.70679	1.00000	0.69332	0.14071
TARL	0.36553	0.36571	0.67075	0.69332	1.00000	-0.05710
CWEI	-0.03313	0.22578	-0.06181	0.14071	-0.05710	1.00000

DETERMINANT OF CORRELATION MATRIX = 0.0000252(.25242405D-04)

Pearson product-moment correlation coefficient matrix of skeletal characters and weight for female House Finches.

	SKUL	SKUW	PREL	PREW	MAND	CORL	STEL	KEED	HUML	ULNL
SKUL	1.00000	0.08100	0.75443	0.61168	0.64237	0.48903	0.34260	0.26508	0.41223	0.40397
SKUW	0.08100	1.00000	-0.03461	0.10371	0.09555	0.22672	0.13508	0.17388	0.02681	0.24967
PREL	0.75443	-0.03461	1.00000	0.40771	0.62257	0.30264	0.12566	0.08335	0.36942	0.31838
PREW	0.61168	0.10371	0.40771	1.00000	0.46897	0.46052	0.26300	0.22881	0.15742	0.16118
MAND	0.64237	0.09555	0.62257	0.46897	1.00000	0.40639	0.20537	0.20884	0.33939	0.38165
CORL	0.48903	0.22672	0.30264	0.46052	0.40639	1.00000	0.63465	0.42739	0.66753	0.68525
STEL	0.34260	0.13508	0.12566	0.26300	0.20537	0.63465	1.00000	0.48847	0.42814	0.34507
KEED	0.26508	0.17388	0.08335	0.22881	0.20884	0.42739	0.48847	1.00000	0.12530	0.05731
HUML	0.41223	0.02681	0.36942	0.15742	0.33939	0.66753	0.42814	0.12530	1.00000	0.81591
ULNL	0.40397	0.24967	0.31838	0.16118	0.38165	0.68525	0.34507	0.05731	0.81591	1.00000
PELL	0.34434	0.05473	0.01962	0.25744	0.13186	0.54387	0.51141	0.26532	0.41228	0.36419
PELW	0.21499	0.08656	-0.01172	0.05681	0.05895	0.29019	0.24497	0.21609	0.20582	0.25724
FEML	0.46981	-0.07024	0.30546	0.15610	0.26571	0.55376	0.42630	0.06449	0.81176	0.75414
TIBL	0.39316	0.09168	0.19733	0.20237	0.28854	0.63409	0.44325	0.23362	0.71302	0.75979
TARL	0.36892	0.06321	0.31639	0.11830	0.26661	0.68450	0.40935	0.04205	0.77526	0.77822
CWEI	0.26336	0.32760	0.06847	0.32897	0.14465	0.40797	0.41176	0.50944	-0.10876	-0.00778

	PELL	PELW	FEML	TIBL	TARL	CWEI
SKUL	0.34434	0.21499	0.46981	0.39316	0.36892	0.26336
SKUW	0.05473	0.08656	-0.07024	0.09168	0.06321	0.32760
PREL	0.01962	-0.01172	0.30546	0.19733	0.31639	0.06847
PREW	0.25744	0.05681	0.15610	0.20237	0.11830	0.32897
MAND	0.13186	0.05895	0.26571	0.28854	0.26661	0.14465
CORL	0.54387	0.29019	0.55376	0.63409	0.68450	0.40797
STEL	0.51141	0.24497	0.42630	0.44325	0.40935	0.41176
KEED	0.26532	0.21609	0.06449	0.23362	0.04205	0.50944
HUML	0.41228	0.20582	0.81176	0.71302	0.77526	-0.10876
ULNL	0.36419	0.25724	0.75414	0.75979	0.77822	-0.00778
PELL	1.00000	0.31909	0.44849	0.33532	0.34734	0.26205
PELW	0.31909	1.00000	0.24325	0.13004	0.06794	0.20664
FEML	0.44849	0.24325	1.00000	0.80977	0.76694	-0.15832
TIBL	0.33532	0.13004	0.80977	1.00000	0.83873	0.00186
TARL	0.34734	0.06794	0.76694	0.83873	1.00000	-0.06922
CWEI	0.26205	0.20664	-0.15832	0.00186	-0.06922	1.00000

DETERMINANT OF CORRELATION MATRIX = 0.0000036(.361933940-05)

Pearson product-moment correlation coefficient matrix of external characters and weight for male House Finches.

	BNL	BIL	BID	BWU	BWL	WLP	WLS	TLL	TSL	CWEI
BNL	1.00000	0.67941	0.37321	0.30674	0.14825	0.01118	0.06581	-0.01980	-0.07918	0.15665
BIL	0.67941	1.00000	0.20026	0.00987	0.08022	-0.20240	-0.18419	-0.27151	0.08927	-0.08648
BID	0.37321	0.20026	1.00000	0.37540	0.33966	0.00751	0.15473	0.05003	0.14324	0.49846
BWU	0.30674	0.00987	0.37540	1.00000	0.46353	-0.17491	0.15605	0.05870	-0.01194	0.47193
BWL	0.14825	0.08022	0.33966	0.46353	1.00000	0.09986	0.17927	0.08764	0.17940	0.19940
WLP	0.01118	-0.20240	0.00751	-0.17491	0.09986	1.00000	0.59552	0.69590	0.02976	-0.15428
WLS	0.06581	-0.18419	0.15473	0.15605	0.17927	0.59552	1.00000	0.69309	0.04343	0.12521
TLL	-0.01980	-0.27151	0.05003	0.05870	0.08764	0.69590	0.69309	1.00000	-0.18201	0.07859
TSL	-0.07918	0.08927	0.14324	-0.01194	0.17940	0.02976	0.04343	-0.18201	1.00000	-0.07641
CWEI	0.15665	-0.08648	0.49846	0.47193	0.19940	-0.15428	0.12521	0.07859	-0.07641	1.00000

DETERMINANT OF CORRELATION MATRIX = 0.0197384(.19738416D-01)

Pearson product-moment correlation coefficient matrix of external characters and weight for females House Finches.

	BNL	BIL	BID	BWU	BWL	WLP	WLS	TLL	TSL	CWEI
BNL	1.00000	0.75199	0.44221	0.38186	0.22413	0.18386	0.29093	0.22715	0.22609	0.22149
BIL	0.75199	1.00000	0.55413	0.30062	0.21644	0.00074	0.21889	0.17940	0.14775	-0.03633
BID	0.44221	0.55413	1.00000	0.39394	0.39276	-0.14878	0.09031	-0.00965	0.16103	0.23850
BWU	0.38186	0.30062	0.39394	1.00000	0.58327	0.10594	0.12938	-0.00646	0.10953	0.47154
BWL	0.22413	0.21644	0.39276	0.58327	1.00000	0.24321	0.23105	0.17425	0.17370	0.47085
WLP	0.18386	0.00074	-0.14878	0.10594	0.24321	1.00000	0.63163	0.69489	-0.05492	0.33948
WLS	0.29093	0.21889	0.09031	0.12938	0.23105	0.63163	1.00000	0.71976	0.01961	0.14542
TLL	0.22715	0.17940	-0.00965	-0.00646	0.17425	0.69489	0.71976	1.00000	-0.25254	0.15988
TSL	0.22609	0.14775	0.16103	0.10953	0.17370	-0.05492	0.01961	-0.25254	1.00000	0.12991
CWEI	0.22149	-0.03633	0.23850	0.47154	0.47085	0.33948	0.14542	0.15988	0.12991	1.00000

DETERMINANT OF CORRELATION MATRIX = 0.0088956(.88955689D-02)

Appendix 7a. Loadings of skeletal characters and weight on the first five principal components of male House Finches from ONT.

	Principal component					
Character	I	II	III	IV	V	Communality
SKUL	0.679	0.396	-0.258	0.262	-0.243	0.812
SKUW	0.379	0.099	0.140	0.868	0.095	0.935
PREL	0.278	0.736	-0.297	0.306	0.098	0.811
PREW	-0.025	0.725	0.199	-0.047	-0.438	0.760
MAND	0.174	0.668	-0.292	-0.388	0.112	0.724
CORL	0.840	-0.132	0.214	-0.173	-0.279	0.877
STEL	0.676	0.488	0.202	-0.226	0.019	0.788
KEED	0.642	0.226	0.561	-0.118	0.113	0.805
HUML	0.879	-0.228	-0.127	-0.119	-0.131	0.872
ULNL	0.870	-0.273	-0.090	0.221	-0.144	0.909
PELL	0.468	0.177	-0.266	-0.095	0.667	0.775
PELW	0.537	-0.158	0.407	0.100	0.345	0.607
FEML	0.693	-0.232	-0.532	-0.232	0.016	0.870
TIBL	0.886	-0.322	-0.057	-0.056	-0.170	0.925
TARL	0.800	-0.142	-0.342	0.056	0.030	0.782
CWEI	0.598	0.045	0.625	-0.138	0.132	0.767
Eigenvalue	6.59	2.35	1.76	1.32	1.02	
% variance explained	41.2	14.7	11.0	8.3	6.4	

Appendix 7b. Loadings of skeletal characters and weight on the first five principal components of male House Finches from CAL.

	Principal component					
Character	I	II	III	IV	V	Communality
SKUL	0.514	0.661	-0.024	-0.183	-0.015	0.735
SKUW	0.080	0.073	0.549	0.660	-0.151	0.772
PREL	0.220	0.637	-0.230	-0.472	-0.336	0.842
PREW	0.345	0.409	0.627	-0.104	0.188	0.725
MAND	0.649	0.587	0.203	0.009	-0.030	0.808
CORL	0.738	-0.395	-0.238	-0.029	0.005	0.758
STEL	0.386	0.401	-0.522	0.457	0.342	0.908
KEED	0.600	0.235	-0.340	0.392	0.280	0.763
HUML	0.782	-0.306	-0.106	-0.210	-0.192	0.798
ULNL	0.813	-0.450	-0.107	-0.072	-0.235	0.936
PELL	0.451	0.287	0.267	-0.155	0.425	0.562
PELW	0.371	-0.238	-0.003	-0.398	0.592	0.704
FEML	0.752	-0.277	0.389	-0.110	-0.087	0.812
TIBL	0.809	-0.263	-0.007	0.160	-0.138	0.768
TARL	0.564	-0.482	0.110	0.197	0.040	0.602
CWEI	0.444	0.549	-0.103	0.151	-0.387	0.681
Eigenvalue	5.26	2.84	1.50	1.40	1.17	
% variance explained	32.9	17.8	9.4	8.7	7.3	

Appendix 7c. Loadings of skeletal characters and weight on the first four principal components of female House Finches from ONT.

	Principal component				
Character	I	II	III	IV	Communality
SKUL	0.692	0.547	0.043	-0.233	0.834
SKUW	0.161	0.151	0.595	0.681	0.867
PREL	0.485	0.599	0.276	-0.376	0.811
PREW	0.419	0.654	-0.227	0.060	0.659
MAND	0.345	0.657	0.407	-0.240	0.773
CORL	0.916	-0.167	0.020	0.089	0.876
STEL	0.804	-0.013	-0.092	0.199	0.694
KEED	0.637	0.345	-0.295	0.011	0.611
HUML	0.885	-0.255	0.114	-0.145	0.883
ULNL	0.803	-0.361	0.353	-0.056	0.903
PELL	0.606	-0.108	-0.488	-0.046	0.619
PELW	0.726	0.058	-0.233	0.320	0.687
FEML	0.798	-0.383	-0.022	-0.343	0.902
TIBL	0.792	-0.310	0.006	-0.023	0.724
TARL	0.756	-0.526	0.191	0.059	0.888
CWEI	0.565	0.420	-0.198	0.458	0.745
Eigenvalue	7.40	2.59	1.25	1.23	
% variance explained	46.3	16.2	7.8	7.7	

Appendix 7d. Loadings of skeletal characters and weight on the first five principal components of female House Finches from CAL.

	Principal component					
Character	I	II	III	IV	V	Communality
SKUL	0.660	0.628	-0.203	0.143	-0.080	0.899
SKUW	0.302	0.084	0.627	0.148	0.613	0.889
PREL	0.454	0.603	-0.438	-0.166	0.139	0.809
PREW	0.669	0.310	-0.444	0.131	-0.005	0.758
MAND	0.758	0.281	-0.289	0.125	0.019	0.753
CORL	0.910	0.158	0.048	-0.043	0.042	0.860
STEL	0.555	0.044	0.322	-0.079	-0.680	0.882
KEED	0.202	0.409	0.664	-0.294	-0.085	0.742
HUML	0.718	-0.483	-0.212	-0.318	0.232	0.949
ULNL	0.780	-0.281	0.064	0.264	0.363	0.893
PELL	0.612	-0.080	0.282	0.390	-0.168	0.641
PELW	-0.323	0.048	-0.013	0.899	-0.070	0.919
FEML	0.745	-0.465	0.044	0.223	-0.194	0.861
TIBL	0.803	-0.452	0.111	-0.044	-0.036	0.866
TARL	0.796	-0.345	-0.020	-0.189	-0.080	0.796
CWEI	0.325	0.707	0.379	-0.028	0.055	0.753
Eigenvalue	6.48	2.50	1.74	1.42	1.14	
% variance explained	40.5	15.6	10.9	8.9	7.1	

Appendix 8. Statistics for morphological characters of nestlings among brood sizes in ONT and CAL: mean, sample size (n), standard deviation.

Character, Nestling age (days)	Locality and Year	Brood size 3	4	5
Weight (g):				
0	ONT 1983	2.06(9)0.38	1.84(35)0.33	1.85(18)0.27
	ONT 1984	2.04(7)0.49	2.19(16)0.37	2.08(14)0.43
	CAL 1984	1.65(6)0.24	1.85(48)0.28	1.69(85)0.24
3	ONT 1983	5.40(12)0.82	5.73(30)1.18	5.57(18)0.32
	ONT 1984	6.19(8)1.37	6.33(16)0.58	5.71(7)1.15
	CAL 1984	4.56(9)1.05	5.03(45)1.03	4.84(62)0.85
6	ONT 1983	11.70(18)1.14	11.70(21)1.97	11.20(19)0.92
	ONT 1984	11.96(6)1.98	11.97(19)0.72	10.69(8)1.39
	CAL 1984	11.07(9)1.50	10.45(56)1.61	9.85(34)1.36
9	ONT 1983	16.30(16)1.22	16.90(17)1.48	15.75(10)0.73
	ONT 1984	16.92(6)0.98	16.13(15)0.80	15.83(3)0.76
	CAL 1984	15.33(3)1.44	15.43(38)1.15	14.22(23)1.41
13	ONT 1983	18.23(10)1.29	18.85(13)1.50	-
	ONT 1984	19.46(7)1.70	20.00(4)0.54	-
	CAL 1984	18.05(5)1.54	17.37(27)0.95	17.11(28)1.13

Bill length (mm):				
0	ONT 1983	2.43(9)0.11	2.39(35)0.11	2.40(18)0.12
	ONT 1984	2.35(7)0.13	2.39(16)0.08	2.40(14)0.09
	CAL 1984	2.20(6)0.05	2.27(48)0.10	2.27(85)0.11
3	ONT 1983	3.17(12)0.23	3.19(30)0.22	3.19(18)0.16
	ONT 1984	3.21(8)0.26	3.28(16)0.17	3.21(7)0.26
	CAL 1984	2.80(9)0.27	3.06(45)0.25	3.03(62)0.22
6	ONT 1983	4.22(18)0.27	4.23(21)0.27	4.14(19)0.17
	ONT 1984	4.21(6)0.40	4.38(19)0.19	4.14(8)0.26
	CAL 1984	4.14(9)0.16	4.02(56)0.26	4.01(34)0.24
9	ONT 1983	5.00(16)0.24	5.06(17)0.23	4.81(10)0.28
	ONT 1984	4.98(6)0.22	5.09(15)0.18	5.03(3)0.06
	CAL 1984	4.98(3)0.28	4.89(38)0.26	4.84(23)0.25
13	ONT 1983	5.97(10)0.26	6.02(13)0.23	-
	ONT 1984	5.95(7)0.20	5.80(4)0.10	-
	CAL 1984	6.01(3)0.27	5.88(27)0.32	5.82(28)0.26
Bill depth (mm):				
0	ONT 1983	2.66(9)0.10	2.54(35)0.15	2.68(18)0.16
	ONT 1984	2.71(7)0.15	2.72(16)0.16	2.71(14)0.15
	CAL 1984	2.51(6)0.11	2.55(48)0.18	2.46(85)0.19

3	ONT 1983	3.33(12)0.22	3.41(30)0.25	3.49(18)0.17
	ONT 1984	3.56(8)0.29	3.63(16)0.21	3.51(7)0.25
	CAL 1984	3.01(9)0.32	3.27(45)0.27	3.24(62)0.23
6	ONT 1983	4.34(18)0.20	4.35(21)0.37	4.39(19)0.16
	ONT 1984	4.45(6)0.28	4.47(19)0.12	4.36(8)0.26
	CAL 1984	4.18(9)0.28	4.06(56)0.27	3.98(34)0.29
9	ONT 1983	5.03(16)0.19	5.04(17)0.21	4.96(10)0.13
	ONT 1984	5.12(6)0.23	4.90(15)0.14	5.05(3)0.13
	CAL 1984	4.58(3)0.19	4.67(38)0.22	4.61(23)0.31
13	ONT 1983	5.71(10)0.19	5.63(13)0.20	-
	ONT 1984	5.86(7)0.30	5.57(4)0.11	-
	CAL 1984	5.40(5)0.27	5.24(27)0.22	5.34(28)0.35
Manus length (mm):				
0	ONT 1983	5.41(9)0.36	5.41(35)0.38	5.21(18)0.22
	ONT 1984	5.50(7)0.35	5.26(16)0.23	5.30(14)0.32
	CAL 1984	5.15(6)0.15	5.39(48)0.30	5.29(85)0.31
3	ONT 1983	8.43(12)0.89	8.62(30)0.98	8.61(18)0.71
	ONT 1984	8.89(8)1.09	8.83(16)0.59	8.66(7)1.11
	CAL 1984	7.44(9)0.79	8.19(45)0.90	8.01(62)0.62
6	ONT 1983	13.39(18)0.96	13.33(21)0.98	13.10(19)0.93
	ONT 1984	12.77(6)0.79	12.71(19)0.75	12.28(8)1.16
	CAL 1984	12.11(9)0.79	12.04(56)1.08	11.68(34)1.08

9	ONT 1983	15.51(16)0.57	15.96(17)0.72	14.66(10)0.67
	ONT 1984	15.31(6)0.60	15.16(15)0.59	14.77(3)0.08
	CAL 1984	14.70(3)0.33	14.55(38)0.69	14.09(23)0.68
13	ONT 1983	16.65(10)0.40	16.94(13)0.87	-
	ONT 1984	16.23(7)0.52	16.24(4)0.58	-
	CAL 1984	15.59(5)0.51	15.42(27)0.47	15.61(28)0.54
Wing length (mm):				
9	ONT 1983	36.72(16)2.73	38.06(18)2.89	34.85(10)2.49
	ONT 1984	35.58(6)2.33	35.73(15)3.14	38.00(3)0.00
	CAL 1984	31.33(3)2.31	35.16(37)2.34	32.86(22)3.08
13	ONT 1983	52.30(10)2.50	53.46(13)2.17	-
	ONT 1984	51.57(7)1.59	47.88(4)1.18	-
	CAL 1984	50.50(5)2.87	50.37(27)2.46	49.82(28)2.77
Tarsometatarsus length (mm):				
0	ONT 1983	5.42(9)0.20	5.47(35)0.28	5.22(18)0.25
	ONT 1984	5.51(7)0.39	5.31(16)0.29	5.41(14)0.39
	CAL 1984	5.16(6)0.23	5.38(48)0.28	5.23(85)0.29
3	ONT 1983	8.74(12)1.04	9.15(30)0.87	8.90(18)0.45
	ONT 1984	8.89(8)1.11	9.13(16)0.77	8.62(7)0.82
	CAL 1984	7.88(9)0.77	8.54(45)0.93	8.35(62)0.70

6	ONT 1983	13.74(18)1.00	13.73(21)0.94	13.71(19)0.64
	ONT 1984	13.53(6)1.27	13.98(19)0.70	13.32(8)1.09
	CAL 1984	13.01(9)0.83	13.27(56)1.01	12.99(34)1.01
9	ONT 1983	16.35(16)0.48	16.91(17)0.73	16.04(10)0.88
	ONT 1984	16.33(6)0.85	16.65(15)0.54	16.25(3)0.22
	CAL 1984	16.17(3)0.12	16.50(38)0.56	16.02(23)0.72
13	ONT 1983	17.02(10)0.53	17.78(13)0.66	-
	ONT 1984	17.74(7)0.36	17.95(4)0.35	-
	CAL 1984	17.58(5)0.75	17.29(27)0.55	17.40(28)0.64

Appendix 9. Statistics for characters of nestlings from hatching (0) to 14 days of age in ONT and CAL: mean, sample size (n), standard deviation.

Character	Age (days)	Locality and year: ONT 1983	ONT 1984	CAL 1984
Weight (g)	0	1.87(62)0.32	2.10(38)0.43	1.75(139)0.26
	1	2.85(70)0.49	3.25(35)0.65	2.49(135)0.41
	2	4.05(67)0.75	4.44(34)0.80	3.63(131)0.67
	3	5.62(60)0.93	6.15(31)0.97	4.89(116)0.94
	4	7.60(58)1.16	7.97(33)1.15	6.58(114)1.11
	5	9.34(61)1.23	9.75(34)1.19	8.38(104)1.33
	6	11.54(58)1.44	11.66(33)1.28	10.30(99)1.55
	7	13.62(47)1.18	13.45(33)1.19	12.21(98)1.55
	8	15.18(46)1.34	14.88(33)1.46	13.73(77)1.46
	9	16.39(44)1.29	16.35(26)0.92	14.99(64)1.37
	10	17.28(39)1.37	17.50(17)0.94	15.88(73)1.27
	11	18.01(34)1.35	17.96(20)1.13	16.56(72)1.27
	12	18.20(33)1.21	19.00(14)1.27	17.00(67)1.25
	13	18.70(29)1.31	19.66(11)1.38	17.30(60)1.10
	14	18.69(18)1.23	20.36(7)0.50	17.40(48)1.02
Bill length (mm)	0	2.40(62)0.11	2.39(37)0.09	2.27(139)0.10
	1	2.59(71)0.14	2.62(36)0.19	2.45(135)0.14
	2	2.85(67)0.18	2.91(34)0.20	2.72(131)0.19
	3	3.19(60)0.20	3.24(31)0.21	3.02(116)0.24
	4	3.54(59)0.24	3.63(33)0.23	3.36(114)0.22

	5	3.88(61)0.22	3.96(34)0.25	3.70(104)0.24
	6	4.20(58)0.24	4.29(33)0.27	4.03(99)0.25
	7	4.50(48)0.22	4.55(33)0.24	4.37(98)0.25
	8	4.80(47)0.21	4.77(32)0.24	4.67(78)0.28
	9	4.98(44)0.26	5.05(25)0.18	4.88(64)0.25
	10	5.25(39)0.27	5.30(17)0.19	5.16(73)0.27
	11	5.49(35)0.27	5.53(20)0.24	5.40(72)0.26
	12	5.73(33)0.25	5.66(14)0.25	5.61(67)0.28
	13	5.97(29)0.24	5.90(11)0.18	5.86(60)0.29
	14	6.21(18)0.21	6.14(7)0.15	6.00(48)0.29
Bill depth (mm)	0	2.59(62)0.16	2.71(37)0.15	2.49(139)0.18
	1	2.85(71)0.20	2.99(36)0.18	2.72(135)0.20
	2	3.17(67)0.25	3.26(34)0.20	2.98(131)0.23
	3	3.42(60)0.22	3.59(31)0.24	3.23(116)0.26
	4	3.82(59)0.25	3.89(33)0.25	3.53(114)0.25
	5	4.15(61)0.24	4.19(34)0.21	3.79(104)0.24
	6	4.36(58)0.26	4.44(33)0.20	4.04(99)0.28
	7	4.61(48)0.17	4.62(33)0.19	4.28(98)0.26
	8	4.81(47)0.17	4.80(32)0.24	4.48(78)0.25
	9	5.02(44)0.18	5.00(25)0.18	4.65(64)0.26
	10	5.20(39)0.21	5.16(17)0.16	4.83(73)0.26
	11	5.36(35)0.18	5.37(20)0.20	5.01(72)0.24
	12	5.52(33)0.21	5.54(14)0.18	5.15(67)0.29
	13	5.64(29)0.20	5.75(11)0.28	5.30(60)0.29
	14	5.84(18)0.14	5.99(7)0.26	5.43(48)0.28

Manus length (mm)	0	5.35(62)0.35	5.32(37)0.30	5.32(139)0.30
	1	6.07(71)0.49	6.08(36)0.51	5.90(135)0.39
	2	7.13(67)0.70	7.28(34)0.66	6.82(131)0.61
	3	8.58(60)0.87	8.80(31)0.84	8.04(116)0.77
	4	10.42(59)1.10	10.23(33)0.80	9.26(114)0.81
	5	12.02(61)1.12	11.58(34)0.82	10.56(104)1.03
	6	13.27(58)0.95	12.61(33)0.86	11.92(99)1.07
	7	14.43(48)0.67	13.70(33)0.76	13.15(98)0.96
	8	15.23(47)0.66	14.42(31)0.62	13.93(78)0.76
	9	15.49(43)0.82	15.12(25)0.57	14.39(64)0.71
	10	15.79(38)0.61	15.44(17)0.52	14.90(73)0.52
	11	16.11(35)0.71	15.76(20)0.42	15.23(72)0.52
	12	16.48(33)0.75	16.02(14)0.49	15.35(67)0.51
	13	16.77(29)0.66	16.23(11)0.51	15.52(60)0.51
	14	16.88(18)0.81	16.16(7)0.38	15.62(48)0.54
Wing length (mm)	7	30.14(7)2.53	30.50(1)0.00	28.11(14)1.16
	8	33.65(31)2.63	32.82(14)1.54	31.02(50)2.02
	9	36.84(44)2.96	35.98(24)2.80	34.16(62)2.88
	10	41.56(39)3.04	39.62(17)2.85	38.81(71)3.08
	11	45.43(35)2.64	44.03(20)3.11	43.06(72)2.87
	12	49.24(33)2.69	47.46(14)2.41	46.58(67)2.63
	13	52.34(29)2.54	50.23(11)2.33	50.13(60)2.61
	14	55.00(17)2.85	52.50(7)2.36	52.96(48)2.40

Tarsomet-atarsus length (mm)	0	5.39(62)0.28	5.38(37)0.35	5.28(139)0.29
	1	6.10(71)0.46	6.27(35)0.52	5.94(135)0.41
	2	7.25(67)0.70	7.45(34)0.66	7.10(131)0.63
	3	8.99(60)0.81	8.96(31)0.88	8.39(116)0.81
	4	10.68(59)0.89	10.83(33)1.01	9.97(114)0.92
	5	12.31(61)1.00	12.40(34)0.88	11.66(104)1.01
	6	13.73(58)0.86	13.74(33)0.93	13.15(99)1.00
	7	15.05(48)0.76	14.90(33)0.90	14.57(98)0.97
	8	16.01(47)0.76	15.80(32)0.76	15.56(78)0.86
	9	16.52(44)0.77	16.53(25)0.59	16.32(64)0.65
	10	16.90(39)0.71	17.08(17)0.41	16.92(73)0.65
	11	17.19(35)0.72	17.30(20)0.54	17.20(72)0.58
	12	17.24(33)0.69	17.56(14)0.36	17.30(67)0.62
	13	17.34(29)0.68	17.81(11)0.36	17.37(60)0.60
	14	17.41(18)0.76	17.89(7)0.36	17.45(48)0.67